11.15

12/22

OUTLINES OF PHYSIOLOGY

IN ITS RELATIONS TO MAN.

PUBLISHED BY
JAMES MACLEHOSE, GLASGOW.

MACMILLAN AND CO., LONDON.
London, ... *Hamilton, Adams and Co.*
Cambridge, . . . *Macmillan and Co.*
Edinburgh, . . . *Douglas and Foulis.*
Dublin, ... *Fannin and Co.*

OUTLINES OF PHYSIOLOGY

IN ITS

RELATIONS TO MAN.

3-6. 81

BY

JOHN GRAY M'KENDRICK, M.D., F.R.S.E.,

PROFESSOR OF THE INSTITUTES OF MEDICINE OR PHYSIOLOGY IN THE
UNIVERSITY OF GLASGOW.

GLASGOW:
JAMES MACLEHOSE, ST. VINCENT STREET,
Publisher to the University.
1878.

To

ALLEN THOMSON, M.D., LL.D., F.R.SS.L.& E.,

PRESIDENT OF THE BRITISH ASSOCIATION FOR THE PROMOTION OF SCIENCE;

EMERITUS-PROFESSOR OF ANATOMY IN THE UNIVERSITY OF GLASGOW;
FORMERLY PROFESSOR OF ANATOMY IN THE UNIVERSITY OF ABERDEEN,
AND PROFESSOR OF THE INSTITUTES OF MEDICINE IN
THE UNIVERSITY OF EDINBURGH,

This Volume is Dedicated

AS A SMALL TOKEN OF GRATITUDE, RESPECT, AND AFFECTION.

PREFACE.

As a Teacher of Physiology, I have felt the practical difficulty of placing before the student a systematic account of the science, as it relates to man, in the course of one hundred lectures. Without the exercise of restraint, there is the risk of being discursive in certain parts of the course, and superficial and meagre in other parts, so that the student obtains what may be regarded as a distorted view of the subject. This danger may be obviated by the use of a text-book which will, by logical arrangement and concise statement of the facts, aid both the Teacher and the Student.

When I consider the limited time at a student's command for the study of each subject in the medical curriculum, I sympathize much with the opinion of the late Mr. Syme that short and concise text-books of the various subjects are of great practical use. The student cannot be expected to be acquainted with the historical development of the subject, nor should his time be occupied with prolonged discussion of theoretical questions, illustrated by conflicting opinions. What he needs is a statement of authenticated facts and generally received principles as these appear to the mind of his teacher.

In writing the following work, I have constantly kept this in view. It does not profess to be more than its title indicates—the "outlines" of human physiology. It contains such a view of the subject as I believe a student of medicine may become acquainted with in his curriculum. If he aspire to honours in physiological science, or if he desire to enter into the consideration of more minute details or of theoretical discussion, he must pass on to such works, in our language, as Dr. Michael Foster's masterly Text-book, or Hermann's Physiology, translated by Professor Arthur Gamgee.

The use of a text-book appropriate to his course may also enable a teacher to develope to a greater extent an effective method of communicating and of testing knowledge. This will be accomplished: (1) by a clear and concise statement of facts; (2) by the experimental demonstration, as far as possible, of these facts; and (3) by frequent oral examination of the students individually.

Two features of this book require a word of explanation. (1) I have avoided the discussion of minute anatomical and histological details, because I regard this as belonging more especially to the province of anatomy. Granting that there is what is termed Physiological Anatomy, it must be evident to all that physiology, as a distinctive subject, is now so largely concerned in the application of physical and chemical truths to the phenomena of the living organism, as to make it desirable to give over to the sister science the description of arrangements of tissues, organs, and of systems which suggest function. At the same time, wherever it was necessary to allude to structure for the intelligent comprehension of function, I have not hesitated to do so.

(2) I have endeavoured to show the student the *methods* by which physiologists have acquired many of the facts of the science; and in doing so, it was necessary to introduce many diagrams of apparatus and of tracings obtained by the

Graphic Method of Registration, which, in the hands of Marey and others, has done so much for physiological science. Some may think that such apparatus ought to be restricted to purposes of research, and ought not to be brought under the notice of the student. The effect, however, will depend on the way in which the latter is attempted. While I recognize the fact that a knowledge of apparatus is not a knowledge of physiology, I am convinced that an intelligent appreciation of the results of physiological research can only be had where the student is shown the method by which these results have been arrived at. In addition, this mode of treating the subject gives it an interest which otherwise it could not possess; it stimulates thought; and its study is an intellectual training of a high order.

I beg to express my obligations to Beaunis' Physiologie, 1876, Wundt's Physiologie, 1872, Brücke's Physiologie, 1875, and to Wundt's Physique Médicale, 1871.

PHYSIOLOGICAL LABORATORY,
UNIVERSITY OF GLASGOW,
April, 1878.

CONTENTS.

GENERAL INTRODUCTION.

CHEMICAL PHYSIOLOGY.

HISTOLOGICAL PHYSIOLOGY.

SPECIAL PHYSIOLOGY.

NUTRITION.

INNERVATION.

LIST OF ILLUSTRATIONS.

The woodcuts for this work were drawn and engraved by MR. STEPHEN MILLER, *North Hanover Street, Glasgow.*

OUTLINES OF PHYSIOLOGY.

GENERAL INTRODUCTION.

Nature and Objects of Physiology—Preliminary Notions of Matter and Force—General Characters of Living Bodies—Distinctive Characters of Plants and Animals—Differentiation of Animal Form—Place of Man in the Animal Kingdom—Varieties of the Human Race.

I.—NATURE AND OBJECTS OF PHYSIOLOGY.

Physiology is the science which treats of the phenomena of living beings. It is divided into Vegetable and Animal Physiology, according as the phenomena of the vegetable or of the animal kingdoms of nature are made respectively the subjects of consideration. The phenomena occurring in man constitute what may be termed Human Physiology, a department of the science which forms the special subject of this treatise.

The physiology of man, or indeed of any living being, cannot be studied with success in an entirely isolated manner; for much of our knowledge depends on the study of operations occurring in a great variety of living beings.

When we study any living being, we observe, first, a peculiar physical structure or conformation of the solid parts; second, a determinate chemical composition of its several solid and fluid parts; and, third, the occurrence of certain chemical, physical, and vital changes.

In the physical structure of the body, certain parts may be readily isolated, and these may each perform a special office in the economy. Such parts are termed *organs*, and the office which each organ performs is called its *function*. *Life*, so far as the individual is concerned, may be said to be the sum of the several functions performed by the various organs, or the active state resulting from their concurrent exercise. (*Allen Thomson.*)

The body may be studied both in the dead and in the living condition. In the dead state its structure and composition are the subject of anatomical and of chemical research. The living state is more especially the province of the physiologist, it being his duty to study the functions or the various phenomena manifested by the organs individually, and as part of a system, during life.

The economy of the human body is one of great complexity, and in its study the physiologist finds it necessary to extend his investigations over a wide field. His information is derived partly from observation and experiments made directly upon man himself, both in the healthy and in the diseased conditions, but very largely also from investigations into the functions performed by the organs of other animals. Many of the facts of physiology with which we are at present acquainted have been derived from observations and experiments made on the humbler animals, but the general plan of structure common to vertebrate animals, and the correspondence in many of the conditions of vital activity, warrant us in applying these facts to our knowledge of the functions of the human body.

Physiology derives its facts from the observation of living phenomena, made with scientific accuracy, and aided by deductions from facts belonging to other branches of science, more especially anatomy, chemistry, and physics. A general acquaintance, therefore, with these sciences is of paramount importance to anyone about to enter upon the study of physiology.

The student ought, in the first instance, to be acquainted with the structure of the human body and of its various organs, and he should also be familiar with the general plan of structure met with in the great general subdivisions of the animal kingdom. Such anatomical knowledge (*Human and Comparative Anatomy*) must be obtained by dissection and by a careful comparison of organs in different groups of animals.

During the past thirty years, much knowledge has been acquired regarding the minute structure of the various tissues forming the body. This constitutes the department of science called *Histology*. As many functions depend on phenomena occurring in elements of the body which are of microscopic size, it is evident that we must be accurately acquainted with the anatomical structure of these elements. Such knowledge, therefore, belongs equally to the anatomist and to the physiologist. The anatomist must describe the form, size, and general relations of these minute parts, while the physiologist directs his attention specially to the phenomena they manifest while alive. Both are engaged in the study of the same textural elements, but from different points of view—the one *morphological*, the other *physiological*. Here, as in the study of parts visible to the naked eye, knowledge of structure and of function are really, in the language of Goodsir, different aspects of the same truth.

To acquire a wide knowledge of the functions of the body, it is not sufficient to study it, even as regards its structure, only in its full-grown or mature condition. It is necessary to examine it at various stages of its development, and to trace minutely the first formation and early development of the embryo, as well as the process of growth of the fœtus and child. This kind of research is included under the name of *Embryology*, and in recent times it has furnished some of the most important information on which the history of vital phenomena is based.

From the facts of *Chemistry* the physiologist derives information regarding the chemical composition of the solid textures, as well as of the various secreted and circulating fluids, and of the variations to which their composition is subject in different conditions of the body. It must be admitted that the chemistry of organic compounds is still in an imperfect state, and that our knowledge of the chemical changes occurring in the living body is still more obscure.

The laws of *Physics* are applied by the physiologist to the investigation of all the obvious motions of solids or fluids occurring in the animal organism. A knowledge of physics is also indispensable in examining the functions of such organs of special sense as the eye and ear, and in studying the influence of light, heat, and electricity, in modifying vital phenomena.

It may further be remarked, that while the researches of the physiologist are directed strictly to establishing the knowledge of the functions of the living economy in a natural condition, or in the state of health, he not unfrequently receives important assistance from the pathologist (*Pathology*), who, by having his attention called to the changes in the exercise of the functions that occur under the influence of different forms of disease, takes advantage as it were of so many experiments made to his hand by nature, and is thus better able to discriminate the share which each particular condition has in the production of these complex results.

The physiological study of the functions of the human body may then be said to consist in the following means of investigation, viz.—(1) The observation of the living phenomena in their natural or healthy state; (2) The occasional comparison of its healthy state with morbid conditions of the economy; (3) The experimental variation in man or animals of the conditions in which the several vital operations take place; (4) The anatomical examination, by dissection and microscopic research, of the structure of the organized parts of the body in the fully-formed state, or at various stages of its growth; and (5) The chemical analysis of the solids and fluids, and of the substances which are taken into or are ejected from the system, and the history of the chemical changes which occur in the living body.

As the object of physiology may be said to be "to ascertain the conditions of body and mind, which are necessary to life, and health," so the most important practical end which the physiologist has in view, in the prosecution of his inquiries, is to furnish data for guiding the physician in detecting diseases with readiness, in distinguishing their different kinds with accuracy, in endeavouring to preserve health, and when disease shall have occurred, to restore the natural condition, and to allay suffering. It is generally admitted that a knowledge of health must precede the advantageous study of disease, and that a rational system of surgical and medical treatment ought to have its foundation in a full acquaintance with the principles of physiology.

Consult ALLEN THOMSON'S Outlines of Physiology.

II.—MATTER AND FORCE.

The permanence of matter and the permanence of force are two great generalizations, the triumphs of modern physical research and thought, which form the groundwork of physical science, and they must be recognized in dealing with the phenomena of the living body just as clearly as in considering the facts of chemistry and physics. In its passage through the living body, matter cannot be created or destroyed; if it apparently disappear, it is only transformed into another condition. The idea of force or energy is inseparable from that of matter; and we must also admit that energy can neither be created or destroyed. It can only be transformed. Energy may be in two conditions, *actual* and *potential.* When actual, energy is being transformed from one condition or state into another; when potential, it is stored up. When energy appears in the actual state, it is as one or other of certain modes which are termed *forces,* and these forces may be transformed the one into the other. Thus mechanical movement may be converted into heat, and heat, on the other hand, may produce movement. The exact relation of two such forces can now be expressed by what is known as the *mechanical equivalent of heat,* calculated by Mayer of Heilbronn, in 1842, and experimentally demonstrated by Joule of Manchester, in 1844. This equivalent may be stated at 425 kilogrammetres, or, in other words, the same force which elevates 425 kilogrammes of water 1 metre in height, in a second, will elevate the temperature of 1 kilogramme of water 1 degree centigrade. Difficulty of experimentation has hitherto prevented the accurate determination of the mechanical equivalent of light, electricity, or magnetism, but we have sufficient evidence of various kinds to entitle us to regard these also as modes of motion, which may be therefore transformed into each other. This great principle is known as the *correlation of the physical forces.* The application of these views regarding energy to living organisms will be shown hereafter.

Certain phenomena occur in the living body which cannot be satisfactorily explained, in the present state of knowledge, by chemical or physical facts or laws. Such phenomena may be conveniently described as *vital*, without necessarily accepting the view that there is a mode of energy termed vital force, as distinguished from the physical forces generally known. The progress of science clearly shows that many phenomena now recognized as physical were at one time held to be vital, and it is highly probable that investigations into the obscure region of molecular physics may enable us to regard phenomena, presently called vital, such as the transmission of a nervous impulse, or the contraction of a morsel of protoplasm, as physical operations. At present this cannot be done; and the physiologist contents himself with studying merely the conditions of such phenomena. These conditions are physical, or chemical, or both. A cell grows and fulfils its functions under certain conditions of pressure, temperature, electrical state, and supply of pabulum, and its growth will be more or less influenced by modifying these conditions. Thus there is a kind of correlation between the physical conditions and the so-called vital phenomena occurring in the cell, but it is not so clearly defined as in the case of purely physical operations, the cause being that at present we do not know the intimate nature of vital phenomena. A firm conviction, however, of the applicability to living beings of the law of the *constancy of energy* is at once a great aid to a clear comprehension of the phenomena of life, and the best guide in future research.

Consult HELMHOLTZ's Lectures on Scientific Subjects, No. 7. TAIT: Some recent advances in Physical Science. JOULE on the existence of an equivalent relation between heat and the ordinary forms of mechanical power. Phil. Mag. XXVIII. MAYER; Die organische Bewegung in ihrem Zusammenhange mit dem Stoffwechsel, 1845. BEAUNIS' Physiologie, Prolégomenes.

III.—GENERAL CHARACTERS OF LIVING BEINGS.

The leading characteristics of living beings may be conveniently considered under the several heads of (1) physical structure, (2) chemical composition, (3) dynamical characters, and (4) evolutional history.

1. *Physical Structure.*—Solid and fluid matters invariably coexist in living bodies; the solids contain fluids in their cavities or interspaces. All the solid parts are more or less moist, and many of them have the character of softness. Living bodies are *organized*, that is, they are composed of dissimilar or distinct parts arranged in a certain order, and each part performs a determinate office or function in connection with the maintenance of the life of the whole. The external form of living beings is consistent with a certain morphological type. At the commencement of existence the typical form is nearly spherical; afterwards in the process of growth, a form is developed peculiar to the species. The spherical form not only is characteristic of the organism at the commencement of life, but is seen also in the primitive elements which compose the organism. This spherical body is called a *cell*, and it may be regarded as the most simple, the most common, and the earliest form of organization met with. Organized matter may also be composed of molecules or granules, fibres, membranes, and tubes. No living matter ever assumes a crystalline form, although crystals may be imbedded in it.

2. *Chemical Composition.*—All organized bodies are heterogeneous and compound; that is, they contain matter in more states than one, and they are composed of a number of chemical elements. Of the sixty-four elementary substances found in nature not more than eighteen or twenty have been discovered in organic matter. Chief amongst these are oxygen, hydrogen, nitrogen, and carbon. The three first are

gases which have never yet been liquefied, a proof of their molecular mobility. Nitrogen is remarkable for its chemical indifference; while oxygen on the other hand, enters readily into combination not only with hydrogen and carbon, but also with nitrogen itself. Along with these are usually associated sulphur, phosphorus, chlorine, sodium, and potassium; others, as calcium, iron, and silicon, are of frequent occurrence; while the remaining elements, fluorine, iodine, bromine, magnesium, manganese, aluminium, copper, and lead, are either found in exceedingly minute quantity, or only in particular plants and animals, in which their occurrence may be looked upon as in some measure accidental.

The simple elements are so combined as to constitute compound bodies which may be separated by chemical processes. These compounds are termed *proximate principles*, and of these the several textures of animals are more immediately composed. Chief amongst these compounds is *water* which constitutes more than three-fourths of the weight of a living body. Certain proximate principles are the same as those met with in the animal kingdom, such, for example, as chloride of sodium, and phosphate of lime. Animal proximate principles are compounds formed by the union of three or four elements, and consequently they are termed *ternary* or *quaternary* compounds. Such are essentially characterized by their chemical instability, which is more marked in the compounds containing nitrogen, a fact possibly due to the presence of that gas. It is well known that nitrogen gives a peculiar instability to certain compounds in which it exists, as for example, in guncotton and nitro-glycerine.

The organic molecule, especially in quaternary compounds, possesses very great complexity.

Living bodies consist largely of *colloids*, a physical condition which Graham has termed the *dynamical state of matter.* Matter in a colloidal condition is non-crystalline, and is permeated readily by water, oxygen, and the *crystalloids,* or bodies which assume a crystalline form. The colloidal state, however, is not peculiar to organic matter, inasmuch as silica and the peroxide of iron sometimes assume this condition.

A living body is continually undergoing a series of chemical changes of composition and decomposition, as a result of which there appears to be an incessant renovation of the molecules of the organism. Chemical changes are a necessary condition of the action of living matter, and part of the living matter dies, is decomposed, and is thrown out of the organism. New matter is added from without, and thus there is a perpetual exchange between the organic and the inorganic worlds, which may be termed the *circulation of matter.*

The mode in which new particles of matter enter a living organism furnishes also a distinctive character. A crystal grows by new molecules, of similar chemical composition to itself, being applied directly to its surface, while a living body absorbs the dead matter into its own substance, and converts what was previously dead into living matter like itself. In other words, dead bodies increase by *apposition;* living bodies by *intussusception.*

3. *Dynamical Characters.*—Living bodies liberate energy in the form of heat, mechanical movement, &c. This liberation of energy, always well marked in animals, is observed in plants only during the formation of the germ, and in germination. Organisms may be regarded as agents effecting a transformation of energy: animals chiefly transform potential into actual energy, while plants are chiefly concerned in reversing the process. Just as there is an incessant exchange between dead and living matter, so there is a perpetual exchange between external forces and the internal forces of the organism. Light, heat, electricity reappear in the living

body under the form of muscular action, of heat, and of nervous energy. The vital movements are thus the correlatives of physico-chemical movements, and the forces called vital may be regarded as the equivalents of physical forces.

4. *Evolutional History of Living Beings.*—The evolution of a living being is determined: it has a commencement, an existence, and an end; it passes through different phases, which succeed regularly and in a certain order. The same statements may be made, with a certain amount of truth, regarding a crystal, but its life history is distinguished from that of a living animal by the absence of waste and of repair, and by its mode of growth, already referred to.

Living beings have a certain individuality. Among the higher grades each member has a certain independence, although related to all; but this characteristic entirely disappears in certain classes of plants and of animals.

All living organisms take their origin in a *germ* which was developed by a parent—that is a previously-existing being having essentially the same structure and properties. Every plant and animal, accordingly, has the power, at one stage of its existence, of producing a germ by which the species may be perpetuated. This germ, which is known as the spore, seed, or egg of plants and animals, is a cell—the simplest form of structure. After its separation from the parent body, it becomes capable of independent existence, and, under favourable external influences, of being converted by growth or development into a new individual, in most respects similar to that from which it derived its origin.

Living beings form a continuous series, from the first appearance of life upon the earth until now. Offspring usually possess more or less of the character of their parents; and they may transmit peculiarities—either acquired by new conditions of existence, or received from their parents—to their descendants. This law is known as *heredity.*

The chemical constitution of a living being varies according to different phases in its evolution. This may be seen by comparing the analyses of a seed with that of a plant, or of an egg with that of an adult animal. This change of chemical constitution during age affects both the quantity and the quality of the proximate constituents. For example, there is a progressive diminution of the amount of water from early life to old age, and it would appear that living organisms towards the termination of life approach inorganic matter in chemical composition. Even in man, advanced years is associated with calcification of cartilage, which impairs the elasticity of the body, and with other changes of a retrograde nature.

The evolution of energy undergoes changes during the life of an organism. Usually the production of energy increases up to a certain maximum, and then slowly declines, so that in the life history of each individual there is a period of *maximum vital activity.* In certain species of animals, however, there are successive phases of repose and of movement, as in the encysted conditions of infusoria, the metamorphoses of insects, and the occurrence of hybernation. In other organisms, also, vital phenomena may appear to be entirely suspended under certain conditions. For instance, some of the *rotiferæ* may be kept in a state of dormant vitality for a considerable time by a simple process of drying.

During the life of an organism it undergoes change of form, increase of its mass, and development of its organization. Death at last necessarily terminates its evolution. When this occurs, the body is submitted to the action of external agencies, both physical and chemical, which ultimately reduce it to the simple elements of which it was at first composed.

It is important to remember that an organism is affected during every instant of its life by the medium in which it lives. The medium furnishes the materials required for existence. Dead matter is supplied to take the place of living matter, and external modes of energy—such as heat and light—are furnished at the same time. There is thus an action and reaction between the organism and the conditions in which it lives. These conditions may be conveniently summarized by the term *environment.* In this adaptation of relations every living organism has a power of suiting itself to modifications of conditions within certain limits. This power is known as its *variability,* and it is a necessary condition of the existence of every living being.

To recapitulate, the essential characters of a living being are the following—

1. Molecular complexity; heterogeneity of parts; and chemical instability of the organic compounds forming it.
2. Waste and incessant repair of organic materials.
3. Production of actual energy in various modes, and, in particular, mechanical movement, heat, and electricity.
4. Organization, or the adaptation of certain parts of the body to particular functions.
5. A regular evolution from origin to death.
6. Origin from a parent, and the possibility of producing the elements of offspring.
7. A power of variability and of adaptation to external conditions.

A discussion of the various theories which have been held regarding the nature of life will be better understood after a description of the chief phenomena manifested by the tissues of which the body is composed.

Consult BEAUNIS' Physiologie. HERBERT SPENCER'S Principles of Biology, vol. I., part I., chaps. 2, 3, 5, 6.

IV.—DISTINCTIVE CHARACTERS OF PLANTS AND ANIMALS.

Life is met with in two principal conditions—the plant and the animal. When we descend among the lower orders of animals and plants it is almost impossible to draw a clear line between the two kingdoms. This difficulty has been felt so strongly by some naturalists as to lead them to group certain organisms in an intermediate kingdom, such as the *protista* of Haeckel. A plant possesses the same fundamental chemical elements as the animal—oxygen, hydrogen, nitrogen, and carbon. It contains more carbon and less nitrogen. Alkalies abound in plants, and phosphates in animals. The chief chemical characteristic of a plant is probably the presence of a colouring matter called *chlorophyll,* which plays a very important part in the life of the plant. One class of plants, however—the fungi—contain no chlorophyll; while on the other hand this substance has been found in certain animals, such as the *Hydra viridis.* The chemical stability of the plant is greater than that of the animal, and chemical transformations are less active in vegetable than in animal textures.

The principal distinctive characters of plants and animals may be briefly summarized as follows—

PLANT.	ANIMAL.
Presence of chlorophyll.	Absence of chlorophyll.
Absorption of water, carbonic acid, and ammonia.	Absorption of oxygen.
Elimination of oxygen.	Elimination of water, carbonic acid, and ammonia.
Feeble liberation of actual energy, as movement and heat.	Intense liberation of actual energy, as movement, heat, and nervous energy.
Transformation of actual into potential energy.	Transformation of potential into actual energy.
Limited locomotive powers.	Usually possess powers of locomotion.

PLANT.	ANIMAL.
No sensibility.	More or less sensibility.
Organization less complex.	Organization more complex.
Tendency to formation of colonies or aggregates of individuals.	Tendency to individualization.
Growth nearly indefinite.	Growth arrested at a given time.
Greater variability to modifications of external conditions.	Less variability.

None of the above characters are absolute. The two kingdoms overlap to a certain extent and present characters common to both.

The nutritional changes occurring in plants and animals are of two kinds—(1) assimilation, and (2) disassimilation; and it is important to observe how plants and animals differ in these operations.

In *assimilation* the organism utilizes or incorporates into its own substance matters which come to it from without. In the case of the plant, these matters are chiefly derived from the air, and consist of water, carbonic acid, and ammonia. Under the influence of sunlight, the chlorophyll of the plant converts these substances into starch, fat, and albuminous bodies, and one of the final effects of this assimilative process is the elimination of oxygen. In the animal the assimilative process is much less complex, inasmuch as it chiefly utilizes the materials previously formed by the plant, and forms only very few complex proximate principles directly from simpler bodies.

By *disassimilation*, on the other hand, is meant the decomposition in the organism of complex substances into simpler ones. It is one of the stages of the waste of materials in the economy, and is directly connected with the evolution of actual energy. Oxygen is introduced, and carbonic acid and water are eliminated. This process, the reverse of assimilation, occurs with great vigour in the animal body, and it is not entirely absent in the plant. All the parts of a plant absorb oxygen and eliminate carbonic acid both in light and in darkness, and the respiration of a plant is therefore an identical process with that of an animal. In plants, however, respiration, which is the introduction of oxygen and elimination of carbonic acid, is carried on to a much less extent than the process of assimilation which, in an actively growing plant, is carried on by the cells containing chlorophyll. Thus, in plants containing chlorophyll the total effect is an absorption of carbonic acid and an elimination of oxygen. From this point of view, a physiological antagonism, as it is often expressed, may be said to exist between animal and plant life.

Consult SACH'S Text-book of Botany, Book I., chap. 1, and Book III., chaps. 1, 2, and 3.

V.—DIFFERENTIATION OF ANIMAL FORM.

If we examine the animal series from the more simple beings to the most complex, the organization is seen to become more and more intricate by nearly insensible transitions. First of all there are unicellular organisms consisting of a simple mass of jelly-like matter called protoplasm; still higher in the scale, the limiting surface of the rudimentary organism acquires a consistence greater than that of the matter in the interior, and thus the protoplasm is enclosed in an envelope called the cell-wall; still higher, certain parts are differentiated for a particular function, as, for example, by the appearance of locomotive organs in the form of cilia, or of reproductive organs such as the nucleus in infusoria. In animals, still higher in the grade, this differentiation of parts affects not only cellular elements, but groups of these elements, so as to produce true organs. Thus a digestive cavity, a circulating organ, a respiratory apparatus, muscles, and organs of sense make their appearance. Such a differentiation of organs and of functions may be followed not only in the animal series, but also in the evolution of an organism. In tracing the development of man himself, we find that he originates in a single cell, the ovum, which represents in this first phase of existence a unicellular animal; this cell divides and multiplies into many cells, forming a multicellular group, somewhat resembling a rhizopod deprived of pseudopodia. Further, one portion of these cells differentiates from the others, and in this portion three layers are formed which, by a continuance of the process of specialization, give origin to all the organs of the body.

Finally, we shall see, in studying the complex organization of man, that in ascending from the lower to the higher forms of life, there is also a gradually-increasing complexity of function.

VI.—PLACE OF MAN IN THE ANIMAL KINGDOM.

Man belongs zoologically to the order of the *primates*. This order comprises five families, namely, (1) *man;* (2) the *anthropoid apes*, including four genera, the gorilla, the chimpanzee, the orang, and the gibbon; (3) the *catarrhines*, or monkeys of the old world, including such forms as the macaque, the cercopithecus, and the cynocephale or baboons; (4) the *platyrrhines*, or monkeys of the new world, such as mycetes, or howling monkeys, the cebus, or capuchin, and the hypale or marmosets; and (5) the *lemurs*. We shall now briefly enumerate the points of resemblance and of distinction between man and the anthropoid apes, to which group in structure and function he is more nearly allied.

Common Characters between Man and the Anthropoids. The organization of the anthropoids is constructed upon the same plan as that of the human being. The vertebral column of the gorilla and of the chimpanzee possesses the same number of vertebræ as that of man. The pelvis, while it is straight and more elongated, has the same general form as the human pelvis, whereas in other apes the pelvis is more like that of quadrupeds. Buffon and Cuvier gave the name of quadrumana to monkeys on account of the superficial resemblance of the foot to the hand; but when the anatomy of the parts is compared, there can be no doubt that the apes, like men, possess two hands and two feet, and are not four-handed.

The brain of man and of the anthropoids presents the four following characters which do not exist in the same degree in other mammalia: (1) a rudimentary olfactory lobe; (2) the posterior lobe of the cerebrum completely covering the cerebellum; (3) the existence of a well-marked fissure of Sylvius; and (4) the presence of a posterior cornua in the lateral ventricle.

The posture of the anthropoids is biped; and the attitude of the body, while it is no doubt oblique, approaches nearer to the vertical than to the horizontal, whereas in the lower monkeys the attitude is decidedly horizontal. The anthropoids are imperfect bipeds. The movements of the upper extremities are analogous to the movements of the arm of man; and the excursion of the hand in supination, which in other monkeys is only to the extent of a right angle, ranges, in the anthropoids, through 180 degrees. (*Goodsir.*)

The resemblance of anthropoid apes to man is most marked in early life. During this stage the young are gentle, affectionate, and intelligent; and the skeleton, and in particular the cranium, presents the general character of the human being; but by degrees, with the approach of puberty, they diverge more and more both in psychical character and in physical conformation from man. Ultimately bestial peculiarities predominate.

Distinctive Characters between Man and the Anthropoids. The capacity of the cranium is much less in anthropoids than in man; the smallest capacity ever observed in man has amounted to 970 cubic centimetres; the greatest found in the gorilla is 539 cubic centimetres; there is thus a difference between the two of 431 cubic centimetres. The difference is more striking when we consider that human crania have been found having a capacity of 1781 cubic centimetres. It thus appears that between human crania at the two ends of the scale, there may be a difference of 811 cubic centimetres, much greater than the difference of 431 cubic centimetres which exist between man and the gorilla.

The *foramen magnum* is situated in the gorilla farther back than in man; the bones of the face, especially the maxillary bones, predominate over those of the cranium; the superciliary ridges are prominent, thick, and arch over the orbital fossa. The facial angle of Camper, which is from 60 to 80 degrees in man, falls as low as 40 and 30 degrees in anthropoid apes in the adult stage, but in the young, it may reach 60 degrees.

The order of closure of the cranial sutures is different: in man the sutures of the base are closed before those of the vault; while, on the contrary, in the anthropoids the frontal suture is closed very early, thus arresting the development of the brain, and the sutures of the base, remaining open for a long time, permit the predominant development of the face.

In anthropoids the canines are largely developed, for purposes of defence, and are lodged, when the mouth is shut, in intervals in the opposite dental arch. The order of appearance of the permanent teeth is not exactly the same as in the human being. Thus in the gorilla, the canines appear after the second and third molars, whereas in man they appear before the eruption of these teeth.

The cerebral convolutions are less developed in the anthropoids, and the layer of grey cerebral matter is much thinner than in man.

Although the hand generally resembles the human hand, the thumb is smaller, and, in the orang, presents the singular peculiarity of having no nail. The carpus of the orang possesses also a supernumerary bone, but the hand of the gorilla is in all respects analogous to the hand of man.

The foot also resembles the human foot, with this difference that the articulation of the great toe is looser and that the first metatarsal, in place of articulating with the anterior face of the internal cuneiform bone, as in man, articulates more with the internal aspect of this bone, and thus permits of a certain degree of movement, though not a true movement of opposition of the great toe.

The gorilla, the chimpanzee, and the orang possess laryngeal sacs, which reinforce the voice, and which are represented in man by the ventricles of Morgagni.

Finally, the proportions of the superior and inferior limbs are different. The following table shows the relative lengths of the arm, the leg, the hand, and the foot, in two varieties of man, and in three of the anthropoids, supposing the length of the vertebral column to represent 100 :—

	European.	Bosjesman.	Gorilla.	Chimpanzee.	Orang.
Vertebral Column,	100	100	100	100	100
Arm, ...	80	78	115	96	122
Leg, ...	117	110	96	90	89
Hand, ...	26	26	36	43	48
Foot, ...	35	32	41	39	52

The differences, however, which distinguish man from all animals are essentially those of an intellectual and moral nature. He possesses to an infinitely greater extent those qualities which are grouped under the general name of *mental.* Thus his pre-eminence consists in the greater extent of his faculties of comparison and invention; in the possession of the power of reasoning; in the employment of language, spoken and written, to communicate his ideas and feelings, and to narrate events; in the development of a moral sense and religious belief; in the power of accumulating, by tradition or written signs, the experience of those who have lived before him; and in the susceptibility, through these different means, of high moral, mental, and religious cultivation, and of social organization. Man reduces external nature and all animals to his service; he is omnivorous, and prepares food by the application of heat and other artificial processes; he is capable of inhabiting all climes, by inventing means to resist the unfavourable influences of external circumstances, notwithstanding the comparatively unprotected condition of his body. (*Allen Thomson.*)

Consult HUXLEY: The Place of Man in Nature. OWEN'S Anatomy of Vertebrates; general conclusions, vol. III. MIVART'S Man and Apes.

VII.—VARIETIES OF THE HUMAN RACE.

The different races of mankind may be classified according to affinities of language, geographical distribution, or anatomical and physiological relationships. Here the latter mode, as more pertinent to the purposes of this work, will be adopted, and, following the classification of Blumenbach, the human species may be divided into five races, namely—

1. *Caucasian or White Races.*—The brain is voluminous, the cranium oval, symmetrical, usually mesocephalic, well developed, and having a capacity of 1,400 to 1,570 cubic centimetres; forehead high and arched; lower jaw small;

teeth vertical; nose more or less straight; the hair soft, fair, or reddish, and having a slight tendency to curl. They inhabit Europe, Arabia, Asia Minor, Persia, Hindostan, and a part of America.

2. *Mongolian or Yellow Races.*—Pyramidal cranium; face large, flat, and having prominent cheek-bones; nose less prominent; yellow eyes, placed somewhat obliquely; hair straight, and usually black; beard feebly developed. The period of puberty is reached at an early age. They inhabit Asia and a part of North America, and include such races as Laplanders, Esquimaux, Chinese, Japanese, and Tartars.

3. *Malay or Brown Races.*—These present variable characters, but usually the cranium is enlarged laterally, and is brachycephalic; the eyes are black, and are largely exposed by retraction of the eyelids; the nose is short; the lips thick; the cheeks and chin are prominent; the hair black and lustrous; and the skin is brown, sometimes tending to yellow and at other times to red. They inhabit Polynesia, the Philippine Islands, the Archipelago of the Pacific, and also Malacca, Madagascar, &c.

4. *American or Red Races.*—The forehead is large, but narrow and retreating, the eyes large and open, the nose long and prominent, the lips thin and delicate, the hair black and soft, the skin red or copper-coloured. They inhabit America, and are usually known by the name of American Indians.

5. *Ethiopian, Negro, or Black Races.*—The brain is small, and the cranium is dolichocephalic; the jaws project, forming a prognathous countenance; the cranial capacity ranges from 1,347 cubic centimetres as a mean, down to 1,228, as found in some Australian races; the forehead is low and retreating, the eyes black and soft, the nose large, the lips thick and prominent; the hair black, coarse, or

woolly; the skin black or brown, the arms long, the foot flat. They inhabit Africa, Australia, Borneo, and Papua.

Although man presents, of all animals, the greatest tendency to occasional variety of structure, and although he is exposed to extreme variations of external circumstances, under the different conditions of savage and civilized life, yet we observe in the human constitution the greatest power of resisting the effect of the variation of external influences, and the greatest functional similarity among races differently situated. As the varieties observed in the organization of men inhabiting different parts of the globe are not greater than what may be supposed to have arisen under the continued influence of difference of climate and other circumstances, and as all the individuals of the most different and of mixed races of mankind are capable of propagating together, all the known varieties of mankind, however dissimilar, may be regarded as belonging to one species. (*Allen Thomson.*)

Consult BLUMENBACH: De Generis Humani Varietate Nativa, 1795. PRITCHARD'S Natural History of Man. PICKERING'S Races of Men. KNOX' Races of Mankind. WILSON'S Prehistoric Man. NOTT and GLEDDON'S Types of Mankind. BÜCHNER: Man in the Past, Present, and Future. Consult also on National Differences of Skull, QUAIN, 8th ed., vol. I., p. 78. An interesting account of the influence of physical agents on the aspect and form of man, and on his intellectual qualities, will be found in DRAPER'S Human Physiology, chaps. 7 and 8.

CHEMICAL PHYSIOLOGY.

Classification of the Elementary Constituents and of the Proximate Principles of the Human Body—General Consideration of the Principal Compounds—Gases of the Human Body—Comparison of the Chemical Composition of Plants and Animals—Chemical Reactions in the Living Body.

I.—CLASSIFICATION OF THE ELEMENTARY CONSTITUENTS AND PROXIMATE PRINCIPLES.

The principal constituents of the human body are divided into (1) elements and (2) compounds.

If a human body were analyzed, the substances obtained would depend upon the methods employed and the extent to which the analysis was pursued. The chemist might resolve it into the elements of which it was composed, or he might separate, or estimate the amount of, the compounds formed by these elements. Compounds exist of greater or less complexity. Thus there are bases and acids, and the salts formed by their union, and there are many organic substances of great complexity, such as albumen, which may resolve themselves, either in the hands of the chemist, or in the laboratory of the living body, into simpler compounds. These remarks will enable the student to comprehend the meaning of the enumeration about to be given of substances found in the body. It is not to be understood that these substances exist in the solids or fluids *as such*, but only that, by various processes, they may be obtained by the chemist from these solids and fluids.

I. ELEMENTS.

Name.	Symbol.	Atomic[1] Weight.	Where found.
Hydrogen, .	H	1	In every tissue and liquid.
Carbon, .	C	12	In every tissue and liquid.
Nitrogen, .	N	14	In many of the tissues ; in solution in fluids.
Oxygen, .	O	16	In all the tissues; in solution in fluids.
Sulphur, .	S	32	Albuminous substances ; blood ; serum of the tissues ; secretions.
Phosphorus,	P	31	Blood ; nervous matter ; bone ; teeth ; fluids.
Fluorine, .	F	19	Bone ; teeth ; traces in the blood.
Chlorine, .	Cl	35·5.	In every tissue and fluid.
Silicon, . .	Si	28	Hair ; blood ; bile ; urine ; epidermis ; saliva ; bone.
Sodium, .	Na	23	Blood ; all the secretions ; serum of the tissues.
Potassium, .	K	39	Muscles ; red blood corpuscles ; nervous matter ; secretions.
Calcium, .	Ca	40	Bones and teeth ; fluids.
Magnesium, .	Mg	24	Bones and teeth ; fluids.
Lithium, .	Li	7	Muscles ; blood ; milk.
Iron, . .	Fe	56	Colouring matter of the blood ; bile; urine; chyle; lymph; sweat; milk.
Manganese, .	Mn	55	Accompanies iron in very minute quantity.
Copper, .	Cu	63·4.	Have occasionally been found in small quantity.
Lead, . .	Pb	207	

II. COMPOUNDS.

These are divided into inorganic and organic.

---

[1] For more accurate atomic weights see Roscoe and Schorlemmer's Treatise on Chemistry, p. 52.

1. INORGANIC COMPOUNDS.

The inorganic consist of water, acids, bases, and salts.

1. *Water* forms about two-thirds of the weight of the body, so that a body weighing about 165 pounds will contain about 110 pounds of water. The following table gives the quantity of water per 1,000 in the principal tissues, organs, and liquids of the human body.

Tissues or Organs.	Water.	Solid Parts.	Liquids.	Water.	Solid Parts.
Enamel,	2	998	Blood,	791	209
Dentine,	100	900	Bile,	864	136
Bone,	220	780	Milk,	891	109
Fat,	299	701	Liquor sanguinis,	901	99
Elastic tissue,	496	504	Chyle,	928	72
Cartilage,	550	450	Lymph,	958	42
Liver,	693	317	Serum,	959	41
Spinal cord,	697	303	Gastric juice,	973	27
Skin,	720	280	Intestinal juice,	975	25
Brain,	750	250	Tears,	982	18
Muscles,	757	243	Aqueous humour,	986	14
Spleen,	758	242	Cerebro-spinal fluid,	988	12
Thymus,	770	230	Saliva,	995	5
Connective tissue,	796	204	Butter,	995	5
Kidneys,	827	173			
Vitreous humour,	987	13			

2. The *inorganic acids* are—

Hydrochloric,	HCl	In combination with sodium everywhere; free in the gastric juice.
Phosphoric,	H_3PO_4	Bones and teeth, and in all fluids.
Sulphuric,	H_2SO_4	Blood, serum, and secretions.
Hydrofluoric,	HF	Bones and teeth.
Silicic,	SiO_2	Hair, epidermis, blood, saliva, bile, and urine.

3. The *inorganic bases* are—

Soda,	Na_2O	Blood, bile, urine, pancreatic juice, and secretions.
Potash,	K_2O	Muscles, red blood corpuscles, nervous matter, milk, and most of the secretions.

Ammonia, . .	NH_3	Traces in the blood and urine.
Lime, . . .	CaO	Bones and teeth; fluids.
Magnesia, . .	MgO	Accompanies lime.

4. The *salts* consist of chlorides, phosphates, sulphates, and fluorides.

Chloride of sodium,	$NaCl$	All tissues and fluids.
Chloride of potassium,	KCl	Blood corpuscles, muscles, nervous matter, secretions.
Chloride of ammonium,	NH_4Cl	A small quantity in the gastric juice, urine, and saliva.
Phosphate of sodium,	Na_3PO_4[1] Na_2HPO_4 NaH_2PO_4	All tissues and fluids, especially in urine and bile.
Phosphate of potassium,	K_3PO_4[1] K_2HPO_4 KH_2PO_4	Accompanies phosphate of soda, and exists also in the red blood corpuscles.
Phosphate of lime,	$Ca_{3}2PO_{4}$ $CaHPO_4$ $Ca2H_2PO_4$[1]	All tissues and fluids, especially bones and teeth.
Phosphate of magnesium,	$Mg_{3}2PO_{4}$	All tissues and fluids, especially in the muscles and thymus gland.
Sulphate of sodium,	Na_2SO_4	Most of the tissues and fluids, especially in milk and bile.
Sulphate of potassium,	K_2SO_4	Most of the tissues and fluids, especially in milk and bile.
Fluoride of calcium,	CaF	Bones, teeth, and blood.

Hyposulphites of sodium and potassium have been discovered in the urine of dogs. The most important of these salts is chloride of sodium, about 200 grammes of which exist in the human body. The following table from Lehmann gives the percentage quantity of chloride of sodium in the principal fluids of the body:—

Blood, . .	0·421 per cent.	Urine, . .	0·332 per cent.
Lymph, . .	0·412 ,,	Saliva, . .	0·153 ,,
Chyle, . .	0·71 ,,	Gastric juice,	0·126 ,,
Bile, . .	0·364 ,,	Milk, . .	0·087 ,,

[1] Very doubtful.

2. ORGANIC COMPOUNDS.

The organic compounds may be first divided into the nitrogenous and the non-nitrogenous.

a. *Non-nitrogenous Compounds.*

These consist of acids, glycogens and sugars, fats, and alcohols.

1. *Acids.*—The principal organic acids are as follows:—

Carbonic,	CO_2	Blood and most fluids, bones, and teeth.
Formic,	CH_2O_2	Spleen, muscles, pancreas, thymus, sweat, blood, urine.
Acetic,	$C_2H_4O_2$	Spleen and muscles.
Propionic,	$C_3H_6O_2$	Sweat, bile.
Butyric,	$C_4H_8O_2$	Spleen, muscles, sweat, urine, blood—sometimes in stomach and intestines, excrements.
Caproic,	$C_6H_{12}O_2$	Sweat.
Caprylic,	$C_8H_{16}O_2$	Sweat.
Capric,	$C_{10}H_{20}O_2$	Sweat.
Palmitic,	$C_{16}H_{32}O_2$	Fat, serum of blood.
Stearic,	$C_{18}H_{36}O_2$	Fat, serum of blood.
Oleic,	$C_{18}H_{34}O_2$	Fat, chyle.
Lactic,	$C_3H_6O_3$	Urine, blood, milk, sweat, gastric juice.
Paralactic,	$C_3H_6O_3$	Muscle serum.
Oxalic,	$C_2H_2O_4$	As oxalate of lime in urine.
Succinic,	$C_4H_6O_4$	Spleen, thymus, thyroid, blood, saliva, urine.
Taurylic,	C_7H_8O	Urine—especially of the cow and of the horse.
Damaluric,	$C_7H_{12}O_2$	Urine—especially of the cow and of the horse.
Cholalic,	$C_{24}H_{40}O_5$	Contained in the great intestine and excrements.
Choloidic,	$C_{24}H_{38}O_4$	Excrements.
Phosphoglycerinic,	$C_3H_9PO_6$	Nervous matter, muscles, blood, urine.

2. *Sugars.*—The glycogens and sugars are—

Glycogen, .	$C_6H_{10}O_5$.	Liver, muscles, skin and chorion of the embryo, lymph corpuscles.
Glucose, . .	$C_6H_{12}O_6$.	Liver, blood, chyle, lymph.
Inosite, . .	$C_6H_{12}O_6 + 2H_2O$	Muscles, liver, spleen, lungs, kidneys, brain, supra-renal capsules.
Sugar of milk,	$C_{12}H_{22}O_{11} + H_2O$	Milk.

3. *Fats.*—The fats found in the body are—

Stearine, . .	$C_{57}H_{110}O_6$.	Fat, and in all the fluids except the urine.
Palmitine, .	$C_{51}H_{98}O_6$.	
Oleine, . .	$C_{57}H_{104}O_6$.	

The quantity of fat in the body may be estimated at about 6 pounds, and this is distributed in the various tissues and organs as follows :—

Cartilage, . .	1·3 per cent.	Hair, ...	4·2 per cent.
Bone, ...	1·4 ,,	Brain, ...	8·0 ,,
Crystalline lens,	2·0 ,,	Spinal cord, .	23.6 ,,
Liver, ...	2·4 ,,	Adipose tissue,	82·7 ,,
Muscles, . .	3·3 ,,	Marrow of bone,	96·0 ,,

4. *Alcohols.*—These are—

Ethyl Alcohol,	C_2H_6O .	Has been found in urine.
Glycerine, .	$C_3H_8O_3$.	Fats.
Phenol, . .	C_6H_6O .	Has been found in urine.
Cholestrine, .	$C_{26}H_{44}O + H_2O$	Nervous matter, blood, and in nearly all fluids.

In addition, two substances of doubtful chemical composition—excretine and dyslisine—have been isolated from the fæces.

b. *Nitrogenous Compounds.*

These may be grouped into acids, bases, amides and neutral bodies, salts, pigments, and albuminous substances.

1. The *acids* are—

Oxaluric,	$C_3H_4N_2O_4$	Urine.
Uric,	$C_5H_4N_4O_3$	Liver, spleen, lungs, pancreas, brain, blood, and urine.
Hippuric,	$C_9H_9NO_3$	Urine of herbivora.
Inosic,	$C_{10}H_{14}N_4O_{11}$.	Muscle serum.
Cryptophanic,	$C_{10}H_{18}N_2O_{10}$.	Urine.
Glycocholic,	$C_{26}H_{43}NO_6$	Bile, and traces in the urine.
Taurocholic,	$C_{26}H_{45}NSO_7$.	Bile, and traces in the urine.
Sulphocyanic,	$CNHS$	Saliva of the parotid gland.

2. *Bases*, *Amides*, and *Neutral Bodies*.

Urea,	CH_4N_2O	Urine, blood, lymph, liver, and sweat.
Glycocine,	$C_2H_5NO_2$	Liver.
Creatine,	$C_4H_9N_3O_2$	Muscles, nervous matter, blood.
Creatinine,	$C_4H_7N_3O$	Urine.
Sarcine,	$C_5H_4N_4O$	Muscles, spleen, liver, supra-renal capsules.
Guanine,	$C_5H_5N_5O$	Pancreas and liver.
Xanthine,	$C_5H_4N_4O_2$	Urine, liver, spleen, pancreas, thymus, brain, muscles.
Leucine,	$C_6H_{13}NO_2$	Pancreas, spleen, thymus, thyroid, salivary glands, liver, kidneys, supra-renal capsules, nervous matter, and lymphatic glands.
Tyrosine,	$C_9H_{11}NO_3$	Spleen, pancreas.
Allantoine,	$C_4H_4N_4O_3$	Urine, liquor-amnii.
Cerebrine.	$C_{17}H_{33}NO_3$	Nervous matter.
Naphtylamine,	$C_{10}H_9N$	Excrements.
Indol,	C_8H_7N	Excrements.
Trimethylamine,	C_6H_9N	Urine.
Cystine,	$C_3H_7NSO_2$	Urine, sweat.
Taurine,	$C_2H_7NSO_3$	Muscles, lungs.
Lecithine,	$C_{44}H_{90}NPO_9$	Nearly all fluids, nervous matter, and semen.
Protagon,	$C_{116}H_{291}N_4PO_{22}$	Nervous matter.

The above formulæ represent the percentage composition of these substances expressed in the simplest numbers, and they throw no light on their actual chemical structure. The analyses of lecithine and protagon are very doubtful.

3. The various organic acids form *salts* by combination with inorganic bases. The principal salts are the following:—

Carbonate of sodium,	Na_2CO_3	Urine and blood of herbivora and omnivora.
Carbonate of potassium,	K_2CO_3	Urine and blood of herbivora and omnivora.
Carbonate of calcium,	$CaCO_3$	Bone, teeth, otoliths, urine of herbivora.
Carbonate of magnesium,	$MgCO_3$	Urine of herbivora.
Hippurate of sodium,	$NaC_9H_8NO_3$	Urine of herbivora.
Hippurate of calcium,	$Ca2(C_9H_8NO_3)$	Urine of herbivora.
Urate of sodium	$NaC_5H_3N_4O_3$	Urine, blood, spleen, liver, pancreas, lungs, brain.
Urate of potassium,	$KC_5H_3N_4O_3$.	
Oxalate of calcium,	CaC_2O_4	Urine.
Glycocholate of sodium,	$NaC_{26}H_{42}NO_6$	Bile.
Taurocholate of sodium,	$NaC_{26}H_{44}NSO_7$	Bile.
Sulphocyanide of potassium,	KCNS	Saliva.

4. The *pigments* which will be described in treating of blood, bile, and urine, are—

Hæmoglobine,	$C_{600}H_{960}N_{154}FeS_3O_{179}$	Blood.
Hæmatine,	$C_{34}H_{34}N_4FeO_5$	Blood.
Bilirubine,	$C_{16}H_{16}N_2O_3$	Bile.
Biliverdine,	$C_{16}H_{20}N_2O_5$	Bile.
Urobiline,	$C_{32}H_{40}N_4O_7$	Urine, excrements.
Indican,	$C_{26}H_{31}NO_{17}$	Urine.

5. *Albuminous Substances.*—These all contain nitrogen and sulphur, and their chemical constitution may be generally represented by the following formula: $C_{54}H_7N_{16}O_{22}S$. Albuminous substances also contain small quantities of

phosphorus which is believed to exist in it as phosphate of lime. The principal albuminates are as follows :—

Albumen of serum,	Blood, lymph, chyle, serum, muscle serum.
Albumen of egg,	White of egg.
Vitelline,	Yolk of egg, and crystalline lens.
Myosine,	Muscle serum.
Fibrinogen,	Liquor sanguinis.
Paraglobuline,	Serum, blood corpuscles, lymph, chyle, crystalline lens.
Fibrine,	Blood, lymph, chyle.
Caseine,	Milk, yolk of egg, serum, chyle, muscle serum.
Syntonine,	Muscle.
Peptones,	A product of the digestion of albuminates.
Mucine,	Mucus.
Keratine,	Epithelium, epidermis, nails, hair.
Collagene or gelatine,	Bone, and connective tissues.
Chondrigene or Chondrine,	Cartilage.

Albuminates exist in the various fluids and tissues of the body in the following proportions per thousand parts :

FLUIDS		TISSUES	
Cerebro-spinal fluid,	0·9	Spinal cord,	74·9
Aqueous humour,	1·4	Brain,	86·3
Liquor amnii,	7·0	Liver,	117·4
Pericardial fluid,	23·6	Thymus,	122·9
Lymph,	24·6	Egg,	134·3
Pancreatic juice,	33·3	Muscles,	161·8
Synovial fluid,	39·1	Crystalline lens,	383·0
Milk,	39·4		
Chyle,	40·9		
Blood,	195·6		

Various substances belonging to the class of ferments are met with in the fluids of the digestive canal, and in the liver.

II.—GENERAL CONSIDERATION OF THE PRINCIPAL CHEMICAL COMPOUNDS.

The physical and chemical characters of the principal organic substances found in the body will be described in an appendix (A), and the chemical composition of the principal tissues and fluids will be referred to in discussing the physiology of the tissues and of the various functions. Here, however, it is necessary to enumerate briefly some of the chief facts of physiological significance regarding the compounds found in the body.

1. Albuminous Substances.

All albuminous substances are amorphous and have a neutral reaction. Their chemical composition, in 100 parts, is 52 to 54 carbon, 7 hydrogen, 15 to 17 nitrogen, 21 to 23 oxygen, and about 1 to 5 sulphur. Their molecular structure is still unknown. The chief albuminous bodies are the following:—

1. *Albumen* is found in white of egg, in serum of blood, in lymph, in chyle, and in all serous effusions. It is coagulated by heat in flakes. In the condition of *vegetable albumen*, it is dissolved in many of the juices of plants.

2. *Caseine.*—This substance is coagulated from milk by heat with the addition of an acid. If any albuminous substance be treated with an alkali, and if the solution be neutralized by acetic acid, a substance chemically identical with caseine is obtained. *Legumine*, found in the grains of leguminous plants, is identical with caseine.

3. *Fibrine.*—This is an albuminous body formed during the coagulation of blood, chyle, or lymph. It is formed by the combination of two soluble albuminoids, *fibrinogen* and *fibrinoplastic substance.* Fibrinogen is found in all fluids

which may transude from the blood into the tissues, in the fluid part of the blood itself, called the *liquor sanguinis*, in lymph and in chyle: whilst fibrinoplastic substance exists in the blood corpuscles and in small quantity in the liquor sanguinis. The conditions favouring the union of these two substances to form fibrine will be described in treating of the coagulation of the blood.

4. *Syntonine* is a jelly-like matter which may be obtained from muscular tissue by the action of hydrochloric acid. It is dissolved by this acid and by weak alkaline solutions, and it is precipitated by neutral salts such as chloride of sodium.

5. *Myosine.*—This substance exists in a fluid condition in living muscle, and, by its spontaneous coagulation after death, the condition called cadaveric rigidity is produced. It may be obtained by pressure from the muscles of a frog recently killed, and it is dissolved in a solution of common salt, a reaction which distinguishes it from syntonine already described.

6. *Globuline.*—This is the albuminous body found in the red corpuscles of the blood. It exists as part of the colouring matter of the blood called hæmoglobine, which will be afterwards described. When it is separated from hæmoglobine, it is recognized by its solubility in water containing oxygen, and by its insolubility in water containing carbonic acid.

7. *Peptone.*—Under this general name we include various substances soluble in water produced by the action of gastric juice on albumen, the characters of which will be described in treating of Digestion.

The principal physical properties of the albuminous bodies are: (1) they are hygroscopic to a remarkable degree; (2) they have the property of deviating polarized light to the left; and (3) they form emulsions with oil, in which, under the microscope, each fatty globule is seen to be surrounded by a thin membrane of albuminous matter.

All these substances are soluble in alkalies and in concentrated acetic acid; they are precipitated by strong mineral acids, tannic acid, metallic salts, and by concentrated solutions of the neutral salts of the alkalies and alkaline earths. In the presence of water and of oxygen, and under the influence of a temperature of from 15° to 40° C., albuminates decompose into a number of products, consisting chiefly of leucine, tyrosine, ammonia, sulphuretted hydrogen, carbonic acid, and the fatty acids.

2. ALBUMINOUS DERIVATIVES.

These are substances closely related to those just described. Among them, we have the intercellular substance found in bone and connective tissue, known as *gelatine* or *collagene*, which is readily obtained from these materials by boiling. Cartilage supplies an analogous body by prolonged boiling, called *chondrine*. In like manner, elastic tissues yield *elastine*; and epithelium, hair, nail, and epidermis yield *keratine*, which is remarkable for its richness in sulphur.

A substance, in the form of colourless crystals, has been obtained from the nervous matter forming the brain and spinal cord, and it has received the names of *protagon*, *cerebrine*, and *myeline*. It has also been discovered in the red corpuscles of the blood, in yolk of egg, and in semen.

Analyses of the albuminous derivatives show that gelatine and chondrine are a little richer in oxygen and a little poorer in carbon than albuminous bodies, whilst elastine contains, on the contrary, more carbon and less oxygen. Gelatine is not precipitated by any acid except tannic acid, while chondrine is precipitated by nearly all acids. Both are soluble in water. Keratine is not dissolved by boiling water or by weak acids, but it is dissolved by alkalies and concentrated acids. Elastine is dissolved only in concentrated alkalies.

The composition of protagon has been represented by the following formula :—

$$C_{116}H_{291}N_4PO_{22}.$$

When boiled with baryta water, it decomposes into phosphoglyceric acid ($C_3H_9PO_6$), stearic acid ($C_{18}H_{36}O_2$), and a very alkaline substance named neurine ($C_5H_{15}NO_2$).

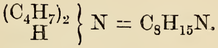
From all secretions of mucous membranes a substance may be readily precipitated, in a flocculent form, by alcohol or acetic acid, which is termed *mucine.* It is difficult to obtain it in a state of absolute purity, and therefore the formula given by Hoppe-Seyler may be regarded as approximative : $C_{52}H_7N_{12}O_{28}$.

3. NITROGEN BASES AND THEIR ALLIES.

When we examine the chemical constitution of plants, we find they contain non-nitrogenous and nitrogenous bodies. As examples of the first, we have (1) carbohydrates, such as cellulose, starch, dextrine, gum, and cane and grape sugar ; (2) the varieties of the essential oils and resins ; and (3) vegetable acids. The nitrogenous compounds comprise the colouring matters of plants, the principal of which is chlorophyll, and organic bases termed *alkaloids.* These bases contain nitrogen, in addition to carbon, oxygen, and hydrogen. The following are examples :—

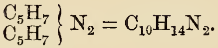
Morphine, . .	$C_{17}H_{19}NO_3$.	Strychnine, . .	$C_{21}H_{22}N_2O_2$.
Conine, . .	$C_8H_{15}N$.	Nicotine, . .	$C_{10}H_{14}N_2$.

Chemically, these bodies are regarded as compound ammonias—that is, bodies in which one, two, or three equivalents of hydrogen are replaced by radicles. Thus conine may be represented as ammonia in which two atoms of hydrogen are replaced by the monatomic radicle C_4H_7, and nicotine as a condensed ammonia in which all the hydrogens are replaced by the triatomic radicle C_5H_7. Example :—



$$\left.\begin{matrix}(C_4H_7)_2\\H\end{matrix}\right\}N = C_8H_{15}N.$$

Conine.



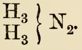
$$\left.\begin{matrix}C_5H_7\\C_5H_7\end{matrix}\right\}N_2 = C_{10}H_{14}N_2.$$

Nicotine.

In the animal economy certain bodies are found which apparently have a somewhat similar chemical structure. They differ in chemical composition from the vegetable alkaloids, however, by containing less nitrogen and oxygen in proportion to the amount of carbon. These substances are—

Leucine, . .	$C_6H_{13}NO_2$.	Creatinine, . .	$C_4H_7N_3O$.
Tyrosine, . .	$C_9H_{11}NO_3$.	Sarcine, . .	$C_5H_4N_4O$.
Glycocine or glycocolle, . .	$C_2H_5NO_2$.	Xanthine, . .	$C_5H_4N_4O_2$.
Taurine, . .	$C_2H_7NO_3S$.	Guanine, . .	$C_5H_5N_5O$.
Creatine, . .	$C_4H_9N_3O_2$.	Allantoine, . .	$C_4H_6N_4O_3$.
		Urea, . . .	CH_4N_2O.

It is probable that certain of these bodies are *amides*—ammonias in which one or more atoms of hydrogen are replaced by radicles of an acid, or *amido-acids*—that is, acids in which one or more hydrogen atoms of the radicle of the acid are replaced by NH_2. Thus urea may be regarded as carbamide—or ammonia containing the diatomic radicle of carbonic acid. Example :—

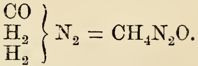


$$\left.\begin{matrix}H_3\\H_3\end{matrix}\right\}N_2.$$

Ammonia.

$CO.$

Radical of CO_2.



$$\left.\begin{matrix}CO\\H_2\\H_2\end{matrix}\right\}N_2 = CH_4N_2O.$$

Carbamide. Urea.

In like manner, on the type of one molecule of water, glycocine may be regarded as amido-acetic acid, leucine as amido-caproic acid, and sarcosine, one of the derivatives of creatine, as amido-methyl-acetic acid. In the amido-acid group of the latter substance one atom of hydrogen is replaced by CH_3 (methyl). Example:—

$\left.\begin{matrix}C_2H_2ONH_2\\H\end{matrix}\right\}O$	$\left.\begin{matrix}C_6H_{10}ONH_2\\H\end{matrix}\right\}O$	$\left.\begin{matrix}C_2HO(CH_3)NH_2\\H\end{matrix}\right\}O.$
or	or	or
$C_2H_5NO_2$	$C_6H_{13}NO_2$	$C_3H_7NO_2$
Glycocine or amido-acetic acid.	Leucine or amido-caproic acid.	Sarcosine or methyl-glycocine, or amido-methyl-acetic acid.

The amides are often conjugated bodies, and they may behave either as bases forming unstable compounds with acids, or they may play the part of feeble acids, which, with the loss of water, unite with alkaline bases. The chief point at present of physiological importance is their instability, especially in the conditions of the living body.

Nearly related to these ammonia bases there are certain compounds known as animal nitrogenized acids, which are divided into two groups.

1. The *Conjugated Biliary Acids*, namely glycocholic acid, $C_{26}H_{43}NO_6$, and taurocholic acid, $C_{26}H_{45}NSO_7$. These compounds are feeble acids, and in the bile exist in combination with sodium. When treated with weak acids or dilute caustic potash, they absorb a molecule of water, and split up into two simpler bodies. Example:—

$$\underset{\text{Glycocholic acid.}}{C_{26}H_{43}NO_6} + H_2O = \underset{\text{Glycocine.}}{C_2H_5NO_2} + \underset{\text{Cholalic acid.}}{C_{24}H_{40}O_5}$$

$$\underset{\text{Taurocholic acid.}}{C_{26}H_{45}NSO_7} + H_2O = \underset{\text{Taurine.}}{C_2H_7NSO_3} + \underset{\text{Cholalic acid.}}{C_{24}H_{40}O_5}$$

It is important to observe that these compounds split up into a nitrogenous and a non-nitrogenous portion. Hippuric acid in like manner may, by the incorporation of water, be resolved into benzoic acid and glycocine. Thus:—

$$\underset{\text{Hippuric acid.}}{C_9H_9NO_3} + H_2O = \underset{\text{Benzoic acid.}}{C_7H_6O_2} + \underset{\text{Glycocine.}}{C_2H_5NO_2}$$

Here again the compound body is resolved into a nitrogenous and a non-nitrogenous portion.

2. *The Non-conjugated Acids.*—Certain acids are also met with in the animal body which are not conjugated, as for example, *inosic acid,* $C_{10}H_{14}N_4O_{11}$, which is found in muscle juice, and the principal acids of urine, namely, *uric acid,* $C_5H_4N_4O_3$, and *hippuric acid,* $C_9H_9NO_3$. Closely related to uric acid, there are a series of bodies sometimes met with in the animal fluids, most of which, by the addition of one or more molecules of water, may be resolved into a nitrogenous base, urea, and a non-nitrogenous acid. Example:—

$C_5H_4N_4O_3$ Uric acid.	+	$4H_2O$	=	$C_3H_4O_5$ Tartronic acid.	+	$2CH_4N_2O$ Urea.
$C_4H_2N_2O_4$ Alloxan.	+	$2H_2O$	=	$C_3H_2O_5$ Mesoxalic acid.	+	CH_4N_2O Urea.
$C_3H_4N_2O_4$ Oxaluric acid.	+	H_2O	=	$C_2H_2O_4$ Oxalic acid.	+	CH_4N_2O Urea.
$C_3H_4N_2O_3$ Allanturic acid.	+	H_2O	=	$C_2H_2O_3$ Oxyglycocholic acid.	+	CH_4N_2O Urea.
$C_4H_6N_4O_3$ Allantoine.	+	H_2O	=	$C_3H_4N_2O_3$ Allanturic acid.	+	CH_4N_2O Urea.
$C_4H_9N_3O_2$ Creatine.	+	H_2O	=	$C_3H_7NO_2$ Sarcosine.	+	CH_4N_2O Urea.

It will be observed that allantoine and creatine split into two nitrogenous compounds. These numerous examples of chemical decompositions are given to show how urea (the principal nitrogenous substance separated by the kidneys) may possibly be produced from more complex nitrogenous substances.

4. NON-NITROGENOUS COMPOUNDS.

These consist of carbohydrates, volatile acids, fatty acids and fats, and non-nitrogenous acids.

1. The *carbohydrates* are *glycogen,* $C_6H_{12}O_6 + 2H_2O$, met with in the liver, blood, and tissues; *glucose* or grape sugar, $C_6H_{12}O_6 + 2H_2O$, found in blood and chyle; *inosite,* or muscle

sugar, $C_6H_{12}O_6 + 4H_2O$, found in muscle; and *milk sugar*, $C_6H_{12}O_6 + H_2O$. It is said that the muscle serum and blood of herbivora often contains dextrine, and it is well known that the bodies of ascidians contain cellulose.

2. The body contains many acids belonging to the group of *volatile* and *fatty acids*. They contain no nitrogen, are met with in most of the secretions, and usually exist in the products of putrefaction of animal tissues. The first in the series have a small, but the last, such as palmitic and stearic acid, have a high, atomic weight. These last enter largely into the structure of the histological elements of animal tissues. The following is a list of these acids:—

Formic acid, . .	CH_2O_2.	Caproic acid, .	$C_6H_{12}O_2$.
Acetic acid, . .	$C_2H_4O_2$.	Caprylic acid, .	$C_8H_{16}O_2$.
Propionic acid, .	$C_3H_6O_2$.	Capric acid, .	$C_{10}H_{20}O_2$.
Butyric acid, .	$C_4H_8O_2$.	Palmitic acid, .	$C_{16}H_{32}O_2$.
Valerianic acid. .	$C_5H_{10}O_2$.	Stearic acid, .	$C_{18}H_{36}O_2$.

With the exception of the four last, all of these acids are liquid at ordinary temperatures, and as their atomic weight increases they become less volatile. Caprylic, capric, palmitic, and stearic acids are crystalline masses. Animal fats contain one or more of these acids, along with butyric acid, and another acid which does not however belong to the same group, oleic acid, $C_{18}H_{34}O_2$.

Composition of a Fat.—Animal fats exist during life in a liquid form, contained in small cells lying in the meshes of connective tissue, from which the fluid may be expelled by pressure. The oils thus obtained have been termed *palmatine*, *stearine*, and *oleine*. Stearine is the most consistent of the three, while oleine is fluid at ordinary temperatures. Human fat is formed chiefly of a mixture of palmatine and oleine, and only a very small quantity of stearine.

Fats consist chemically of a combination of a triatomic alcohol known as *glycerine*, $C_3H_8O_3$, with a fatty acid. Their structure may be best comprehended by supposing that they are built on the type of three molecules of water, in which three of the hydrogens are replaced by three atoms of the monatomic radicle of a fatty acid and the remaining three by the triatomic radicle glyceryl. Thus:—

$$\underset{\text{Radicle.}}{C_{16}H_{33}} \quad - \quad H_2 + O \quad = \quad \underset{\text{Radicle of palmitic acid.}}{C_{16}H_{31}O}$$

$$\underset{\text{Radicle.}}{C_{18}H_{37}} \quad - \quad H_2 + O \quad = \quad \underset{\text{Radicle of stearic acid.}}{C_{18}H_{35}O}$$

$$\underset{\text{Water.}}{(H_2O)_3} \quad \underset{\substack{\text{Radicle of}\\ \text{palmitic acid.}}}{C_{16}H_{31}O} \quad \underset{\text{Glyceryl.}}{C_3H_5} \quad \Big\} \underset{\text{Palmitine.}}{(C_{16}H_{31}O)_3C_3H_5} \Big\{ \; O_3 \text{ or } C_{51}H_{98}O_6$$

$$\underset{\text{Water.}}{(H_2O)_3} \quad \underset{\substack{\text{Radicle of}\\ \text{stearic acid.}}}{C_{18}H_{35}O} \quad \underset{\text{Glyceryl.}}{C_3H_5} \quad \Big\} \underset{\text{Stearine.}}{(C_{18}H_{35}O)_3C_3H_5} \Big\{ \; O_3 \text{ or } C_{57}H_{110}O_6$$

$$\Big\} \underset{\text{Oleine.}}{(C_{18}H_{33}O)_3C_3H_5} \Big\{ \; O_3.3H_2O \text{ or } C_{57}H_{104}O_6 + 3H_2O$$

A fat may thus also be considered as a compound-ether, or, in other words, as consisting of palmitic, oleic and stearic glycerides, variously mixed together.

3. The *non-nitrogenous acids* have been already referred to. They exist in very small quantity in the animal body, whereas they are found abundantly in plants. One of the most important is *cholalic acid,* $C_{24}H_{40}O_5$, which, by uniting with glycocine and taurine, forms the conjugated biliary acids as already described. It is found in small quantities in the intestinal canal. *Lactic acid,* $C_3H_6O_3$, is the only acid of low atomic weight which is of importance in the animal economy. It exists in the gastric and intestinal juices in the ordinary condition, and it is found somewhat modified in muscle serum, where it is known as *paralactic acid.*[1]

---

[1] As to the differences between these acids, see p. 83.

III.—GASES OF THE HUMAN BODY.

The gases of the human body consist of oxygen, nitrogen, carbonic acid, hydrogen, carburetted hydrogen, and sulphuretted hydrogen. These gases exist either free in certain cavities of the body or are dissolved in certain fluids.

1. Free Gases.

1. *Oxygen* is found in the pulmonary passages, and in the intestinal tube. The oxygen of the lungs comes directly from the atmosphere of the air; while that of the intestinal tube, which is in small quantity, is no doubt introduced with food and drink.

2. *Nitrogen* is also found in the lungs, and in the intestinal canal. According to Chevereul, the great intestine contains usually more than the small intestine, a fact which would indicate that a portion of the nitrogen may be derived from another source than atmospheric air.

3. *Hydrogen* has been found in small quantity in the air of expiration, and also in the intestinal canal; it is said to increase in the great intestine during a milk diet, and to reach a minimum during a meat diet. Its origin in the intestine is probably due to fermentation.

4. *Carbonic acid* also exists in the lungs and intestinal canal. In the lungs it is derived from the blood, and in the intestinal canal it may come partly also from this source, but is no doubt chiefly due to chemical decomposition.

5. *Carburetted hydrogen* has been found in the great intestine, where it is said to exist to the amount of from 5 to 10 per cent. It is increased by a leguminous, and falls to a minimum during a milk, diet. It is the result of decomposition.

6. *Sulphuretted hydrogen* is occasionally found in the

intestinal canal, and results from the decomposition of the albuminous elements of food, or from biliary matters, both of which contain sulphur.

2. Gases in Solution.

Oxygen, nitrogen, and carbonic acid exist partly in solution, and partly in a state of loose chemical combination, in all the fluids of the body. The chief facts will be described in treating of the various fluids. Reference is made to tables on page 44, compiled from various authorities, which give the quantity of gas contained in the principal fluids.

IV.—COMPARISON OF THE CHEMICAL COMPOSITION OF PLANTS AND ANIMALS.

The following are the principal points to be noted :—

1. The albuminoid substances are nearly identical in plants and animals.

2. The substances known as albuminous derivatives, which form a constituent portion of the tissues of animals, such, for example, as gelatine, chondrine and elastine, are not met with in plants; while mucilaginous and fermentive substances, which resemble these derivatives, are met with in both kingdoms.

3. By the decomposition of albuminous substances, various nitrogenized products or bases may be formed both in plants and animals. In plants, these bases are peculiar to the species, as for example the alkaloids of opium; whereas they are nearly identical in all the different species of animals.

4. Vegetables are richer in non-nitrogenous substances than animals, and the most of those which exist in animals, such as sugar, fats, and non-nitrogenous acids, are also found

TABLE I.—QUANTITY OF GAS, IN CUBIC CENTIMETRES, CONTAINED IN 100 CUBIC CENTIMETRES OF THE FLUID. (*Beaunis.*)

NAME OF GAS.	Arterial Blood.	Venous Blood.	Serum.	Lymph.	Fluid from Ascites.	Bile of Dog (1).	Bile of Dog (2).	Saliva of Dog.	Urine.	Serum of Muscle.	Albumen of Egg.	Pus.	Milk.
Carbonic acid,...	50	60	50·00	46·90	142·00	7·36	73·81	74·93	18·09	15·40	66·76	75·28	10·00
Nitrogen, ...	2	2	2·00	1·67	21·10	0·78	0·52	0·92	1·21	4·90	3·77	2·50	1·05
Oxygen, ...	20	10	1·47	0·13	0·14	0·00	0·26	0·65	0·10	0·09	2·31	...	0·11
Hydrogen,........	...	...	...	...	...	...	...	...	...	...	...	5·16	...
Total,.........	72	72	53·47	48·70	163·24	8·14	74·59	76·50	19·40	20·39	72·84	82·94	11·16

TABLE II.—QUANTITY OF GAS, IN CUBIC CENTIMETRES, CONTAINED IN 100 CUBIC CENTIMETRES OF GAS. (*Beaunis.*)

NAME OF GAS.	Arterial Blood.	Venous Blood.	Serum.	Lymph.	Fluid from Ascites.	Bile of Dog (1).	Bile of Dog (2).	Saliva of Dog.	Urine.	Serum of Muscle.	Albumen of Egg.	Pus.	Milk.
Carbonic acid,...	69·46	83·55	94·54	96·30	87·00	90·33	98·95	97·93	93·20	74·30	91·66	90·77	89·51
Nitrogen, ...	2·77	2·77	3·15	3·43	12·92	9·67	0·70	1·20	6·23	25·20	5·17	3·01	9·42
Oxygen, ...	27·77	13·88	2·31	0·27	0·08	0·00	0·35	0·87	0·57	0·50	3·17	...	1·07
Hydrogen,........	...	...	...	...	...	...	...	...	...	...	...	6·22	...

(1) Dog fed with an animal diet. (2) Dog fed with vegetable diet.

in plants. On the other hand, plants contain many non-nitrogenous substances never met with in animals, such as cellulose, gums, essential oils, resins, and vegetable acids.

5. The fluids of vegetables hold in solution oxygen, carbonic acid, and ammonia; while the fluids of animals contain only oxygen and carbonic acid. The fluids of plants contain more carbonic acid, and those of animals more oxygen.

6. Both plants and animals contain various inorganic salts, consisting chiefly of the alkaline chlorides, and of the alkaline and earthy phosphates, which exist in about equal proportions. It has been asserted that in plants the chlorides and phosphates may more easily be substituted the one for the other than in animals.

V.—CHEMICAL REACTIONS IN THE LIVING ORGANISM.

Hitherto we have been describing the substances obtained by chemical processes from dead animal matter, or from the secretions or excretions of the body. It is manifestly a much more difficult task to attempt to follow the chemical reactions which occur in the living body, and it may be at once admitted that much of our knowledge of such phenomena is based upon inferences collected from the general facts observed by the physiological chemist when he analyzes the substances obtained from the body, and studies how they are affected by oxidizing and deoxidizing agents, into what simpler substances they may be decomposed, or what more complex substances may be formed by their combination. We are still ignorant of the exact phenomena and conditions of those obscure chemical processes which occur in living tissue, and which appear to be absolutely necessary for the manifestation of vital action, inasmuch as it is impossible to submit living tissues to the ordinary processes of chemical analysis, even on a microscopic scale, without destroying their vitality.

The principal chemical reactions, however, may probably be classed into the three great divisions of analytical processes, synthetical processes, and fermentations.

1. Analytical Processes.

The analytical processes occurring in the living body consist of oxidations, reductions, and decompositions.

a. *Oxidations.*

Oxidations are the most common chemical reactions in the living organism. The albuminates, fats, and carbohydrates, by union with oxygen, form a series of compounds, somewhat simpler in chemical composition, and lower in molecular weight than themselves. From these, by a continued process of oxidation, bodies still less complex in chemical composition are formed, and so on in successive stages until the elements which at first existed in albuminates now appear under the form of urea, carbonic acid, and water, and those of the carbohydrates and fats as carbonic acid and water. At present it is impossible to demonstrate the successive phases through which albumen may have to pass, but there is little doubt that many of these have been observed by chemists in the laboratory. Thus, by oxidation, albumen has been resolved into leucine, tyrosine, glycocine, and fatty acids; uric acid into urea, allantoine, oxalic acid, and carbonic acid; guanine into xanthine, oxaluric acid, and urea; creatine into sarcosine and urea, and fats into the whole series of fatty acids. It has also been found that the introduction into the living body of one or other of these substances has been followed by the appearance in the secretions of an increase of the materials into which this body may be resolved. Thus, the introduction of uric acid increases the amount of urea and of oxalate of lime excreted.

The oxygen of the air introduced by respiration is the agent which effects the oxidations; but it is remarkable, that while in the laboratory these oxidations only take place at a high temperature and slowly, in the living condition they occur at the temperature of the body and with much greater rapidity. To explain this, it has been assumed that the oxygen of the tissues is in the condition of ozone, which is known to have strong oxidizing powers even at comparatively low temperatures. On the oxidation processes occurring in the body, animal heat, mechanical work, and innervation largely depend.

b. *Reductions.*

The phenomena of reduction which is so important in the life of a plant, do not occur so frequently in the animal body. The formation of fat from carbohydrates is an example: the carbohydrates lose oxygen, and become transformed into fats. The formation of indol, C_8H_7N, and of trimethylamine, C_6H_9N, bodies which are occasionally found in small quantities in animal fluid, have been supposed to be due to a process of reduction.

c. *Decompositions.*

By decompositions we mean the splitting up of an organic substance into two or more chemical compounds, the combined molecular weight of which is exactly equal to the molecular weight of the first substance. Thus taurocholic acid may divide into choloidic acid and taurine.

$$\underset{\text{Taurocholic acid.}}{C_{26}H_{45}NSO_7} = \underset{\text{Taurine.}}{C_2H_7NSO_3} + \underset{\text{Choloidic acid.}}{C_{24}H_{38}O_4}$$

Occasionally, by dehydration or the removal of water, a simpler body may be formed. Thus, with the aid of heat, cholalic acid may be converted into dyslysine and water, and creatine into creatinine and water.

$$\underset{\text{Cholalic acid.}}{C_{24}H_{40}O_5} = \underset{\text{Dyslysine.}}{C_{24}H_{36}O_3} + 2H_2O$$

$$\underset{\text{Creatine.}}{C_4H_9N_3O_2} = \underset{\text{Creatinine.}}{C_4H_7N_3O} + H_2O$$

Sometimes a molecule of water may be removed, and the residue may then split up into simpler compounds. Thus, oxalic acid may be divided into carbonic acid, carbonic oxide, and water.

$$\underset{\text{Oxalic acid.}}{C_2H_2O_4} - H_2O = CO_2 + CO$$

It would appear in some instances that a compound must combine with water before splitting up. This occurs in the saponification of fats and in the decomposition of glycocholic acid into cholalic acid and glycocine.

$$\underset{\text{Glycocholic acid.}}{C_{26}H_{43}NO_6} + H_2O = \underset{\text{Cholalic acid.}}{C_{24}H_{40}O_5} + \underset{\text{Glycocine.}}{C_2H_5NO_2}$$

In like manner, creatine may be resolved into urea and sarcosine, and urea into carbonic acid and ammonia.

$$\underset{\text{Urea.}}{CH_4N_2O} + H_2O = CO_2 + 2NH_3$$

2. SYNTHETICAL PROCESSES.

The formation of organic substances by synthesis in the living animal body is still very imperfectly understood, but it is interesting to observe that many nitrogenous organic compounds have been formed synthetically by the chemist in the laboratory. Thus urea, hippuric acid, glycocine, taurine, sarcosine, creatine, and oxalic, lactic, succinic, benzoic, propionic, acetic, and formic acids, have been formed artificially; but as yet it has been impossible to prepare the higher members of the series. It is probable that in the living body more of the nitrogenous compounds are formed by analytical than by synthetical processes. One well-known example of a synthetical process is the formation of hippuric acid after the introduction of benzoic acid with food or medicine. In these circumstances, benzoic acid unites with glycocine to form hippuric acid, which makes its appearance in the urine.

$$\underset{\text{Benzoic acid.}}{C_7H_6O_2} + \underset{\text{Glycocine.}}{C_2H_5NO_2} = \underset{\text{Hippuric acid.}}{C_9H_9NO_3} + H_2O.$$

3. FERMENTATIONS.

Certain substances have been long known to possess the property of exciting chemical changes in matters with which they come into contact. Such substances have been named by chemists *ferments*, and the process is known as *fermentation.* As fermentation plays a very important part in nature, and as in recent times it has been supposed to be the explanation of many processes occurring in the body, and to account for the origin of not a few forms of disease, namely, those included under the generic name of zymotic, it is necessary to refer to it here somewhat in detail.

Fermentations may be divided into two classes, according to the nature of the agents exciting the process. These are (*a*) soluble and (*b*) organized ferments.

a. *Soluble Ferments.*

The soluble ferments are those which are the products of secretion, or of chemical changes in animal or vegetable cells, and, as examples, may be taken diastase of malt, and ptyaline found in saliva. When obtained pure, they are solid, amorphous, colourless, tasteless bodies, soluble in water, and precipitated from their aqueous solutions by alcohol, and the acetates of lead. Chemically, they resemble in constitution the derivatives of albuminates, but they contain no sulphur. The following are a few examples of fermentive processes:—

1. The conversion of starch into dextrine, and glucose, produced by the action of the diastase of malt; of ptyaline in saliva; of a ferment in the pancreatic juice; and of all albuminous matters in a state of decomposition.

2. The tranformation of cane sugar into inverted sugar, which is a mixture of dextrose and laevulose, and into glucose accomplished by a ferment in the intestinal juice, and perhaps by a ferment in yeast.

3. The conversion of glucosides, such as amygdaline, into glucose and various compounds, accomplished by synaptase or emulsine.

4. The conversion of glycerine and mannite into glucose, said by Berthelot to be effected by a ferment obtained from the tissue of the testicle. (Watt's Dictionary of Chemistry —Art. *Mannite.*)

5. The conversion of glycerine and of mannite into alcohol by the action of nitrogenous organic matter in a state of decomposition.

6. The splitting up of fats into fatty acids and glycerine by the action of a ferment in the pancreatic juice.

7. The transformation of albuminates into peptones by the action of pepsine, the ferment of the gastric juice, and by a ferment in the pancreatic and intestinal juices.

The following are examples of the chemical changes effected in these processes of fermentation—

1. Simple isomeric transformations, as in the conversion of starch into dextrine and sugar.

2. Hydrations, as in the conversion of cane sugar into glucose.

3. Synthetic processes, as in the fermentation of glucosides.

4. The separation of water, and a change in the molecular condition of the remainder, as in the conversion of albuminates into peptones (*hydrolytic ferments*).

It is to be noted that, in many instances, chemical changes, similar to those produced by soluble ferments, may be effected by the action of heat and of the mineral acids. Fermentations of this class are the principal agents in the chemical transformation of food in the process of digestion, and in all probability processes of a fermentive character also occur in certain organs, as in the liver.

b. *Organized Ferments.*

These are living organisms, the type of which is the unicellular plant found in yeast, and known as *Torula cerevisiæ*, and including such organisms as many forms of fungi, vibrios, and bacteria. It is not within the province of this work to describe these organisms, or to enumerate the products which are formed by them. It will be sufficient to point out some of the facts of their history, which are of biological importance.

1. Soluble ferments usually produce, as the result of their action, not more than one or two substances, but the organised ferments, as a rule, produce several substances. Thus glucose, in the presence of yeast, not only may yield carbonic acid and alcohol, but also glycerine, succinic acid, acetic acid, fatty matter, a nitrogenous matter, and other products.

2. Organized ferments do not absolutely require the presence of the oxygen of the air, as they have the power of obtaining oxygen from fermentiscible matter itself. In certain cases it would even appear that excess of oxygen arrests fermentation. Pasteur has shown that vibrios are killed by a strong current of oxygen passed through the fluid contain-

ing them, and Paul Bert has found fermentation to go on much more slowly under a pressure of five atmospheres of pure oxygen.

c. *Theories of Fermentation.*

In all fermentations there are two results—first, a change in the matter undergoing fermentation; and, second, a constant increase of the ferment itself when the conditions are favourable. Fermentation is usually accompanied by an absorption of oxygen and an elimination of carbonic acid. All organized ferments possess a strong affinity for oxygen. When they receive their oxygen from the atmospheric air, they may be termed *ferments of oxidation*, and when they have the power of removing it from the fermentiscible substances, *ferments of reduction.*

The reducing power of ferments is very variable. They may be able to reduce the binoxide of hydrogen, H_2O_2, into water and oxygen, and in certain conditions they may even decompose water into its elements. The most energetic of all processes similar to fermentation is that of chlorophyll in vegetable cells, which can decompose carbonic acid and water, and under the influence of light, can form, from the elements of these, organic compounds, especially carbohydrates. Fermentations which are accompanied by oxidation, have sometimes been grouped under the name of *putrefaction*, to distinguish them from true fermentations, which are chemical processes consisting simply of decompositions without oxidation. The same ferment, however, by reason of its strong affinity for oxygen, may reduce another substance and at the same time absorb the oxygen thus set free. Usually, organized ferments which produce these two actions present different forms. Thus, the ferment of true fermentations appears under the form of small isolated cells, which remain in the deeper part of the fluid in which they exist; while, on the contrary, the organisms which produce putrefaction are composed of chains of small cells, of various forms, which chiefly float upon the surface of the fluid. These latter constitute the *moulds* which appear frequently on the surface of organic fluids or on damp surfaces. They belong to the division of *fungi* (Pencillium, Aspergillus, Mucor, &c.).

The following four hypotheses have been offered to explain the phenomena of fermentation :—

1. *Contact theory.*—The ferment possesses an unknown action, termed *catalytic*, by which simple contact with the fermentive substance excites decomposition. (Berzelius.)

2. *Mechanical theory.*—Ferments are bodies in a state of intense molecular movement, and these movements may be transmitted to organic matter so as to excite in them a tendency to decomposition. It will be observed that this theory somewhat resembles the contact theory, and gives no satisfactory explanation of the phenomena.

3. *Vitalist theory.*—Fermentations are always excited by organisms. This theory has derived much support in recent years from the elaborate researches of Pasteur, and is the one now most generally accepted. The theory of Pasteur is that the air contains the germs of microscopic plants and animals; and when these germs find a fitting soil, they develop themselves therein, producing fungi and infusoria which excite fermentation.

4. *Physico-chemical theory.*—This view, strongly advocated by Liebig, is that there is no necessary connection between the fermentive process and the development of living organisms, and that the organisms may simply produce a substance, the molecular vibration of which may cause a rearrangement of the atoms of the substance undergoing fermentation. This is a modification of the mechanical theory above described. The splitting up of sugar into

carbonic acid and alcohol, by the action of the yeast plant, he places side by side with the decomposition of anhydrous acetic acid into acetone and carbon dioxide (a change brought about by heat), and with the change of an aqueous solution of cyanogen gas into oxamide, which is brought about by the action of the merest trace of aldehyde. Just as the vibration produced by the aldehyde determines the rearrangement of the atoms of cyanogen and water so as to constitute oxamide, so Liebig regards the rearrangement of the atoms of sugar as the result of a vibration produced by the chemical changes which take place in some unstable substance produced by the yeast-plant. The growth of the yeast-plant is, according to this idea, indirectly connected with the process of fermentation. "It is possible," he says, "that the physiological process stands in no other relation "to the process of fermentation than that, by means of it, a "substance is formed in the living cell, which, by an action "peculiar to it—resembling that of emulsin on salicin or "amygdalin—determines the decomposition of sugar and "other organic molecules. In such a case, the physiological "action would be necessary for the production of this substance, but would be otherwise unconnected with the "fermentation properly so called." (Article "Fermentation," in Supplement to Watt's Dictionary of Chemistry.)

It is asserted that in the fermentive process excited by soluble ferments, such as the conversion of albuminates into peptones by the action of pepsin, the amount of ferment at the end of the process is the same as at the beginning. This statement, however, does not necessarily involve the idea that in the process the ferment undergoes no change, and that its influence is mysteriously due to some kind of contact action. It is more reasonable to suppose that the action is due to reciprocal exchanges between the ferment and the fermentible matter, as is illustrated in the continuous etherification process caused by the action of sulphuric acid upon alcohol, for an account of which reference is made to any textbook on organic chemistry.

In considering the mode of action in organized ferments, it is impossible at present to say whether (1) they produce soluble ferments which excite changes in the fermentescible matter, or (2) whether the products of fermentation are the results of nutritional processes of absorption and of excretion carried on by the living organism or cell which we regard as the ferment.

Consult BEAUNIS' Physiology; Chimie Physiologique. GERHARDT: Chimie Organique. HOPPE-SEYLER, Handbuch der Physiologisch- und Pathologisch-Chemischen Analyse. MILLER'S Chemistry, vol. III. KÜHNE: Lehrbuch der Physiologischen Chemie, 1868. GORUP-BESANEZ: Lehrbuch der Physiologischen Chemie, 1874. HERMANN'S Physiology, translated by GAMGEE; Chemical Constituents of the Human Body. FOSTER'S Physiology, p. 493.—On Fermentation, consult PASTEUR: Annales Chimiques et Physiologiques, 3rd series, lviii. 323, lii. 404. BERZELIUS: Jahresberichte, xx. 454. MILLER'S Chemistry, vol. III. BERTHELOT: Chimie Organique Fondée sur la Synthèse. Articles "Fermentation," in WATT'S Dictionary of Chemistry, vol. III. and Supplement.

HISTOLOGICAL PHYSIOLOGY.

The Cell and Protoplasm—The Connective Tissues—Epithelium—The Contractile Tissues—The Cartilaginous and Osseous Tissues—The Nervous Tissues—Diffusion and Endosmotic Action in Tissues—Vital Phenomena of Tissues—Law of the Constancy of Energy, and its Application to Living Tissues.—Theories of Life.

All the tissues and organs of the body originate from an embryonic *cell* termed the ovum. After fecundation this cell divides into numerous cells, and these are developed into *tissues*. The various tissues combine to form *organs*, which are parts of the body differentiated for a special purpose in the economy. The organs of animals are never formed by a single tissue, but one kind of tissue usually predominates and determines the principal functions of the organ, while at least two others are present as accessory structures. Groups of organs constitute a *system* which manifests functions of greater complexity than that of a single organ. The organs forming a system are more or less dependent on each other, and on the organs of other systems. The different systems found in the body may be grouped as follows—(1) The *osseous system*, which forms the frame-work of the body; (2) The *muscular system*, by which cavities are formed, and the various parts of the skeleton are more or less moveable upon each other; (3) The *digestive and visceral system*, specially connected with the preparation of matter for the nutrition of the body; (4) The *vascular system* for the distribution to every tissue and organ of a nutritive fluid, and for the removal of waste products ; (5) The *nervous system*, which not only regulates and physiologically connects all the others, but is associated with sensation, volition, and intellectual acts ; and (6) The *reproductive system*, for the perpetuation of the race. An account of the structure and relations of these various systems forms the subject of descriptive anatomy.

In this section we shall first describe the physiology of the cell, the simple element from which all tissues are derived, and of protoplasm, its principal constituent. This will lead the way to a consideration of the physical and physiological properties of the various tissues, without entering into detail regarding their minute structure more than is necessary for the comprehension of their functions. There are numerous details of structure, the results of recent histological investigation, which at present have no physiological significance. These are fully described in recent works on histology.

I.—THE CELL AND PROTOPLASM.

The *cell*, according to the original definition of Schleiden and Schwann, the founders of the theory that all the tissues are derived from cells, is a small microscopic vesicle, composed of a membrane, the *cell wall*, enveloping some semi-fluid matter, the *cell contents*, in which are embedded a small, round, or oval body, the *nucleus*, in which there may be a still smaller body, the *nucleolus*. Research has shown, however, that neither the cell wall nor nucleus are essential portions of a body which possesses all the physiological peculiarities of a cell, which thus is reduced to a more or less homogeneous mass of organized matter named *proto-*

plasm. Before entering on the consideration of the phenomena of cell life, it is necessary to describe the general characters of protoplasm.

1. PROTOPLASM.

This is a jelly-like substance, colourless, or faintly yellow, amorphous, or having embedded in it molecules or granules. It is difficult to observe it in the ultimate structures of the higher animals, and our knowledge of it has been derived chiefly from observations on microscopic animals and plants. It may be met with in nature in two conditions—(1) free, or (2) in the interior of cells. Free protoplasm may occur in masses of jelly-like matter, called *plasmodies,* as may be seen in *myxomycetes,* which are the fungi found on old leather, or on tan. Such masses, when examined under the microscope, are granular, and show not only changes of form slowly occurring, but also currents flowing through the jelly-like matter in various directions. It has been ascertained that these movements are affected by external agents. Thus the protoplasm moves towards light; heat quickens while cold retards the movements, and extreme cold or extreme heat will arrest the movements altogether; electricity excites contraction; oxygen, as in atmospheric air, is necessary for the movement, and excess increases its activity; and finally, the movements are arrested by carbonic acid, ether, chloroform, solutions of sulphate of quinine, and by other poisons.

Another form of free protoplasm is seen in the *amœbæ* of stagnant pools. These consist of a mass of protoplasm, sometimes homogeneous, but usually containing granules. These bodies slowly change their form, pushing out one part of the body in a particular direction as a perfectly hyaline substance, and afterwards slowly retracting it. Sometimes numerous processes are thus protruded simultaneously, or one after the other, so as to give the mass of protoplasm an irregularly stellate appearance. By these changes of form the amæba moves from place to place. It may also surround by these processes any particle of nutrient matter with which it may come into contact, and afterwards absorb it into its substance. Bodies exactly similar to the amæba, and therefore called *amœboid*, exist in the body, as, for example, the colourless corpuscles of the blood and connective tissue corpuscles.

Protoplasm may also exist in the interior of vegetable and animal cells. Thus its movements may be watched in the hairs of *Tradescantia*, and of *Urtica*, the common nettle, and in the cells of *Chara* and *Vallisneria*. These movements, which are usually in a determinate direction in the interior of the cell, constitute what is termed *cyclosis*. The existence of protoplasm may also be demonstrated in many animal cells, such as in the cartilage cell, in the pigment cell of the frog's skin, in the ovum, and in the bodies of many cellular infusoria.

The jelly-like matter which forms the organic basis of protoplasm is nitrogenous, and is probably of an albuminous nature, while the granules consist of fats or starch. The identity of protoplasm in animal and vegetable cells has been assumed but has never been proved. Protoplasm is permeable by water. The molecular changes occurring in it are very active. It assimilates and excretes and it absorbs oxygen and eliminates carbonic acid. So far as our present methods of research carry us, the liberation of energy in protoplasm occurs under the form of movement. This movement presents itself under two aspects: (1) a kind of liquefaction, as it has been called, which produces the optical appearance of a current in the mass; and (2) a change of form which, in some cases, produces a movement of progression. In certain masses of protoplasm there exist small cavities filled with water, called *vacuoles*, the walls of which frequently show rhythmical contraction.

2. The Cell.

This structure has already been generally described, but attention must now be more particularly directed to its different parts.

1. *The Cell Wall.*—In very young cells there is frequently no cell wall, but as age advances the external layer of protoplasm is differentiated into a more or less resistent membrane, which is homogeneous, amorphous, and transparent. Sometimes it possesses a certain amount of elasticity so as to mould itself upon the surface, when the included protoplasm changes its form, but at other times it is stiff and rigid. It is permeable by water and by aqueous solutions of acids, bases, and salts, but it will not permit the passage of oils and fatty substances. Its chemical constitution is not the same in the animal and vegetable kingdom. In plants it is formed of cellulose, a non-nitrogenous substance; but in animals it is always nitrogenous. It contributes only to the life of the cell by its physical property of permitting the passage of fluid by osmosis, but it is not connected in any other way with the vital phenomena of the cell. Occasionally it may become hard and impermeable by the deposit in it of calcareous salts and of silica.

2. *The Cell Contents.*—This, which is the essential portion of the cell, has been already studied in treating of protoplasm. The cell may also contain fluids and certain matters peculiar to it, such as fat, pigment, or chlorophyll.

3. *The Nucleus* is a small body situated usually in the centre, more rarely in the periphery, of the cell. It has been supposed to be of the nature of mucine, but this is very doubtful. It is not always present, and multiplication of the cell contents may take place without its presence, but in vegetable cells the nucleus always precedes the formation of the cell.

4. *General Characters of Cells.*—The size of animal cells varies from $\frac{1}{12000}$ to $\frac{1}{200}$ of an inch in diameter. The ovum is the largest known cell, and is visible to the naked eye. While the typical form is spherical, the cell may be ovoid, fusiform, cylindrical, polyhedral, or flattened. The form would appear to depend largely on the amount and direction of the pressure to which the cell is subjected. The most important physical character of the active cell is its permeability to fluids. If cells are placed in distilled water, they swell out by imbibition; on the other hand, if placed in a fluid of greater specific gravity than that of their contents, they may shrivel and become irregular in form by the passage of a portion of their contents into the surrounding fluid.

5. *Nutrition of the Cell.*—The nutritional changes of the cell consist of assimilation and disassimilation. By assimilation the cell receives from the medium which surrounds it certain materials which it converts into its own proper substance, or which it may utilize in various ways. There appear to be two phases of the assimilative process—(1) one in which the cell transforms the matter which it receives, and the other (2) in which the substances transformed become an integral part of the cell. The first phase is well marked in the life of the vegetable cell, but is not so distinct in the animal cell, which in a manner lives upon materials previously formed by the plant; the second phase, on the contrary, exists to an equal extent both in the animal and vegetable cell. The assimilating power of the living portion of the cell has received the name of *metabolisis*, while the chemical changes by which matters taken up by the cell may be converted into other matters is called *metastasis.* Thus a cell may, by metabolic processes, convert dead matter into living matter like itself, or it may, by metastatic processes, convert dead matter into another form. (See Sach's Botany, p. 626.) The disassimilative processes occur-

ring in the living cell consist of an oxidation of the substance of the cell itself, or of materials in contact with the cell, a chemical change which leads to the manifestation of energy. Disassimilative processes constitute a marked feature in the life of animal cells. Certain cells have the property of separating or forming a special kind of material. Thus some cells form fatty matter, others pigment, and a third, one or other of the substances existing in bile. This power has been termed *elective affinity*, a phrase which is only another mode of expressing the fact. Certain materials are separated from cells by a process which may be termed *cellular excretion*, and other cells may store up certain materials in their interior, a process called *cellular secretion*.

6. *Irritability of Cells.*—By this term we mean the aptitude which a cell has of responding to a determinate stimulus, and which is an important condition of vital phenomena. The stimulus may be mechanical, chemical, physical, or vital, by the latter term meaning such an excitation as may be conveyed by the nervous system. The same kind of stimulus may produce different results, varying according to the nature of the cell. Thus the response to a stimulus of a muscular cell is contraction; to a glandular cell, secretion; to an epithelial or connective tissue cell, cell multiplication; and to a nerve cell, some kind of activity resulting in sensation, perception, volition, or one or other of the stages of intellectual acts. It may be laid down as an axiom that no activity in a cell ever occurs without an antecedent stimulus.

Each cell is to a certain extent independent of the other and of the organism. It possesses a life of its own which may exist for a time even after the death of the organism as a whole, and on the other hand it may be said that the life of the organism is the sum of the lives of its component cells.

7. *Cell Movements.*—Cells manifest certain movements which may be conveniently divided into two groups:—

(*a*) *Intra-cellular Movements,* which are seen in the protoplasm of Tradescantia, already referred to, in the molecular movements of the salivary cell, and in the movements in pigment cells first observed by Joseph Lister.

(*b*) *Movements of the whole Cell.*—Of these there are four kinds: (1) amæboid movements, as in the colourless corpuscles of the blood; (2) contractile movements affecting the whole cell, as in muscular fibre; (3) vibratile movements of a portion of the cell, as seen in cilia; and (4) the movements of locomotion, in which the cell is moved as a whole, seen in the migratory cells of connective tissue and in spermatozoids.

8. *Genesis of Cells.*—Great discussions have taken place amongst physiologists as to the possibility of the formation of cells in an amorphous matter in which no cells existed. The majority adopt the doctrine briefly enunciated by Virchow—*Omnes cellula à cellula,* which is a parody of the more famous biological dictum of Harvey—*Omne vivum ex ovo.* Without denying the possibility of free cell formation in certain circumstances, it may be safely asserted that the development of cell from cell is now the more common process. Cells may multiply in the following manner:—

(*a*) *Endogenous Cell Formation.*—This method is only presented in cells having a cell wall. The nucleus and the protoplasm divide into two distinct masses, each of which may afterwards become a distinct cell. The nucleus becomes constricted, and by degrees may be divided into two or more portions. The protoplasm then divides in a similar manner, and there may result 2, 4, 8, 16, &c., cells, in each of which there is at least one nucleus. Such a process is termed *segmentation,* and may be seen in the early stages of the development of the embryo. The cell wall may persist and increase in capacity so as to contain a number of cells, but a time arrives when the cell wall ceases to grow, ruptures, and sets free the new cells.

(*b*) *Fissiparous Cell Formation or Fision.*—This is also a process of segmentation which, however, includes the cell wall (if it exist) as well as the protoplasm. Thus, two or more cells may be formed by division of the body of the parent cell.

(*c*) *Gemmiparous Cell Formation or Budding.*—In this mode, at certain points in the generating cell, minute processes or buds make their appearance, which, increasing in size, may become nearly as large as the parent cell, and may be united with it only by a pedicle. The pedicle gives way, and the new cell begins an independent existence. This mode of cell formation may be well studied in the development of the yeast-plant, and is quite common amongst the lower organisms. It has less frequently been met with in the tissues of the higher animals.

9. *Evolution of Cells.*—Each cell may be regarded as an organism which has a determinate period of existence. The duration of life is very variable. Some, such as epithelial cells, may pass through existence in from twelve to twenty-four hours; those of the mammary gland may have a more transitory existence; whilst such cells as those of cartilage probably exist during the life-time of the individual. Cells die in various ways. They may be mechanically removed from the superficial surfaces, as is the case with epidermic cells; or they may undergo chemical transformations of such a nature as to be inconsistent with the vitality of the cell. For instance, as frequently happens in pathological conditions, the cell may become infiltrated with calcareous, fatty, or amyloid matter. Sometimes, also, cells may break down, molecule by molecule, undergo liquefaction, and be absorbed.

Consult SCHLEIDEN: Beitrage sur Phytogenesis (Archiv. für Anat. 1838). SCHWANN: Mikr. Untersuchungen, &c., 1838. For an account of the views of SCHLEIDEN and SCHWANN, see Brit. and For. Med. Rev., vol. IX., and their works translated by the Sydenham Society. Article on the General Characters of Cells, STRICKER'S Human and Comparative Histology, vol. I. M. SCHULTZE: Das Protoplasma, 1863. W. KÜHNE: Untersuch. über das Protoplasma, 1864. GOODSIR'S Anatomical and Pathological Observations. CH. ROBIN: Anatomie et Physiologie Cellulaires, 1873. R. VIRCHOW'S Cellular Pathology, translated by CHANCE. BENNETT'S Text-book of Physiology, pp. 50-60. BEALE: On the Structure of the Simple Tissues, London, 1861; Protoplasm, London, 1870. QUAIN'S Anatomy, 8th ed., vol. II., p. 8 *et seq.* Consult, also, as to Molecular Movements, RAINEY, On the Mode of Formation of Shells of Animals, of Bone, and of several other structures, by a process of molecular coalescence, &c., 1858. LISTER: On the Cutaneous Pigmentary System of the Frog, Phil. Trans., 1858. MONTGOMERY: On the Formation of So-called Cells, by Protagon, &c., 1867.

II.—THE CONNECTIVE TISSUES.

By this term is understood a group of tissues consisting of cells lying in or amongst an amorphous or fibrillary intercellular matter. Although, in the fully-developed condition, many of the tissues composing this group are very unlike each other, in the embryonic state they all consist of cells. It is not the object of this work to enter into histological details, and it will be sufficient to give here a classification of the different forms of connective tissues, and afterwards to describe their chemical, physical, and vital characters.

1. CLASSIFICATION OF CONNECTIVE TISSUES.

1. *Proper Connective Tissues*—
    - *a.* Mucous tissue, as in the vitreous humour.
    - *b.* Adenoid or reticulated tissue, as existing in lymphatic glands.

- *c.* White fibrous tissue, as existing in tendons, aponeurosies, and cellular tissue.
- *d.* Adipose tissue, as in fat.

2. *Yellow Elastic Tissue,* as seen in ligamentum nuchæ, and in blood vessels.

3. *Cartilaginous Tissue*—
   - *a.* Hyaline cartilage, as seen on articular surfaces.
   - *b.* White fibro-cartilage, as in intervertebral discs.
   - *c.* Yellow fibro-cartilage, as in epiglottis.

4. *Osseous Tissue*—
   - *a.* Bone.
   - *b.* Dentine of tooth.

2. CHEMISTRY OF CONNECTIVE TISSUES.

When ordinary connective tissue is submitted to prolonged boiling, it yields gelatine of which it principally consists. In addition, it contains a small quantity of albuminoid matter, salts, and fat. Adipose tissue, as the name implies, is formed chiefly of fat. Adenoid or embryonic tissue, and the vitreous humour, do not contain gelatine, but a substance analogous to mucine. Elastic tissue consists almost entirely of elastine. The chemical composition of cartilage and of bone will be given in describing these substances.

3. PHYSICAL PROPERTIES OF CONNECTIVE TISSUES.

1. *Specific Weight or Density.*—This varies within wide limits, of which the extremes are adipose tissue and bone. The lightness of adipose tissue, which is largely employed in the body as a protective substance for delicate organs, is of importance as it diminishes the total weight of the body, and, consequently, the muscular force required to move it.

2. *Consistence.*—This varies from a diffluent or semifluid

state as in the vitreous humour, to considerable hardness as in bone. The consistence depends upon the amount of water contained in the substance. Thus, the vitreous humour contains about ninety-eight, and bone about three per cent., of water.

3. *Cohesion.*—This depends upon the adhesion of the molecules forming the tissue, or the union side by side of the fibres composing it. The amount and direction of the cohesion may be indicated by the manner in which the tissue yields to force. Thus, costal cartilage will break more easily in the transverse than in the longitudinal direction, while in such structures as tendon it is more easy to separate the fibres from each other than to break them across. The forces which act upon connective tissues, and which are resisted by their cohesion, are traction or pulling, pressure, and flexion, and torsion. Bone and tendon present great resistance to traction. Thus the tendon of the plantaris muscle of man will support a weight of about fifteen kilogrammes without breaking. By resistance to traction the tendons and ligaments accomplish a certain amount of mechanical work; sometimes the membranes formed by the connective tissues afford support to groups of muscles, or assist in giving strength to the walls of cavities. Resistance to pressure is well marked in the flat bones, in the intervertebral discs, and in the cartilage covering articular surfaces. It thus assists in the maintenance of posture, and in walking. Resistances to pressure and torsion are only exerted in certain circumstances. For example, when the hand supports a heavy weight, the arm being horizontal, the bone tends to become bent; in inspiration, the costal cartilages and ribs undergo torsion, which ceases during expiration, when the cartilages and bones return to their previous condition. The connective tissues also give cohesion to the various organs.

4. *Elasticity.*—This property includes (1) the change of form of an elastic body under the action of some force; and (2) the return of the body to its original form when this force ceases to act. Elasticity may be perfect or imperfect, and it may be great or small. Lead is very elastic, but its elasticity is imperfect; indiarubber, on the contrary, is feebly but perfectly elastic. The elasticity of a body may be measured by the weight necessary to effect the change of form. The connective tissues may be divided, with reference to their elasticity, into two groups—(1) Yellow elastic tissue, which is feebly but perfectly elastic, that is, it changes its form under the influence of a feeble force, and returns exactly to its original form; (2) The second group includes connective tissue properly so-called, namely, tendons and ligaments, which are highly but imperfectly elastic—that is, they change form only under the action of powerful forces, and do not return completely to their original state. The elasticity of connective tissues plays a very important part in the body—(1) It is a permanent force which resists other permanent forces, such as gravity or muscular action. Thus the elasticity of the intervertebral discs, and of the *ligamenta sub flava*, assists in maintaining the erect position of the vertebral column, and in expiration the elasticity of the costal cartilages and of the ribs restores the original form of the thorax when the inspiratory muscles have ceased to act. (2) Elasticity transforms an intermittent into a continuous movement; thus, the elasticity of the arterial walls converts the intermittent flow of the blood in the arteries into a continuous current.[1]

The endosmotic properties of the connective tissues will be described in treating of the influence of endosmosis on the nutrition of all the tissues.

---

[1] As to influence of elasticity of muscle, see p. 99.

4. VITAL PROPERTIES OF CONNECTIVE TISSUES.

1. *Nutrition.*—The nutrition of connective tissues is usually feeble, except during the process of growth. Some varieties are richly supplied with vessels, as, for example, white fibrous tissue, while others, such as the vitreous humour and cartilage, are non-vascular. The latter are nourished by imbibition; the fluid part of the blood, destined for nutrition, permeating their substance, and supplying the materials necessary for repair. The waste products are removed chiefly by the radicals of the lymphatic system.

2. *Sensibility.*—This is usually feeble. The marrow and periosteum of bone contain numerous nervous filaments, which occasionally manifest extreme sensibility, as during the process of inflammation.

Regarding the Histology of the tissues, consult QUAIN'S Anatomy, vol. II., by SHARPEY and SCHÄFER, p. 52; and FREY'S Histology, p. 164. And as to Physical Properties, consult BEAUNIS' Physiologie, p. 224. WUNDT'S Physiologie, p. 38. W. WEBER: Ueber die Elasticität fester Körper (Poggendorf's Annalen, 1841). ED. WEBER: Muskelbewegungen in WAGNER'S Handwörterbuch d. Physiologie, III., 2nd part. WERTHEIM: Mem. sur l'Élasticité et la Cohésion des Principaux Tissues du Corps Humain (Annales de Chim. et de Phys., 1847). WUNDT: Ueber die Elasticität feuchter Organischen Gewebe (Muller's Archiv., 1857); Physique Médicale, p. 69.

III.—EPITHELIUM.

Epithelium consists of one or more layers of actively-growing cells on one surface of a homogeneous membrane: numerous bloodvessels ramify on the other surface. The term *endothelium* has been recently applied to the lining membrane of the shut cavities of the body, such as the pleura, peritoneum, &c.; but as its etymological meaning is quite inaccurate it is better to abandon its use. Epithelial cells may be either spherical, irregularly cylindrical, polyhedral, or flattened in form. They may exist in one or more layers, and they appear to be cemented together by some kind of intermediate substance. When the cells are flattened, irregular in form, and exist in a single layer, as in the pleura and peritoneum, the intermediate substance is demonstrable by the action of certain re-agents, especially a solution of nitrate of silver, which, when applied in certain conditions, blackens the intercellular matter. The following varieties of epithelium are met with in the body :—

1. *Simple, flat, squamous*, or *tesselated epithelium*, in which there is scarcely more than a single layer of developed cells, such as is observed on the internal surfaces of the serous and synovial membranes, and on those of the heart, bloodvessels, and absorbent vessels. This is the variety incorrectly termed *endothelium* as above explained.

2. *Laminar* or *stratified epithelium*, consisting of a number of flattened cells, usually in various stages of alteration, such as exist in the epidermis and on the mucous membranes near the entrance of the alimentary and genito-urinary passages. Nails, hair, and horns are modifications of this texture.

3. *Columnar* or *prismatic epithelium*, consisting of a single layer of elongated nucleated cells ; below these, however, are in general seen others of a more spherical shape, which are, in fact, the columnar particles in an earlier stage of growth. Such is the structure lining the whole alimentary canal, from the cardia downwards, and also part of the ducts of secreting glands.

4. *Spheroidal epithelium* may be regarded almost as belonging to the last mentioned form ; it constitutes, in some places, a transition form between the columnar and tesselated varieties ; it is best seen in the urethra, ureters, and pelvis

of the kidney, and also in the ducts of the mamma, and of the cutaneous and some other glands.

5. *Ciliated epithelium* is generally of the columnar form, and consists of nucleated cells, upon the free surface or ends of which minute microscopic hair-like projections or *cilia* are placed, which, when covered with fluid, move with great rapidity. This kind of epithelium lines all the air passages, and the cavities and passages communicating with them, such as the nasal ducts, the conjunctiva of the eye-lids, the sinuses opening into the nasal passages, the Eustachian tube and tympanum, part of the soft palate and pharynx; also the uterus and Fallopian tubes, and the ventricles of the brain.

Each of these forms of epithelium has a special function. Tesselated epithelium covers an extensive surface for protective or absorptive purposes; columnar epithelium has numerous cellular elements on a surface of limited extent, so as to permit great nutritive vitality; stratified epithelium, from the abundance of cells, admits of the rapid growth and shedding of these for functional purposes; and ciliated epithelium maintains vibratile movement.

Epithelium forms a continuous layer over the surface of the body, and lines all the internal passages and cavities. This fact is of physiological importance, inasmuch as it indicates that all substances entering or leaving the body must, in some way or other, pass through an epithelial layer.

1. PHYSICAL PROPERTIES OF EPITHELIUM.

Where epithelium is exposed to pressure and other external influences, it becomes more or less hard and firm, as may be seen in the nails, in the epidermis covering the palms of the hands and soles of the feet, in "corns," and in the callosities which appear on the hands of those performing much manual labour. The columnar epithelium of the intestinal canal is, on the contrary, soft and easily detached. The cohesion of epithelium is usually feeble, but such structures as the epidermis may sustain considerable distension without rupture, as may be seen over large abdominal tumours. Elasticity is very imperfect. An epithelial layer is a bad conductor of heat and electricity. The hairy covering of many species of animals, and the feathery covering of birds, by diminishing the amount of heat lost by radiation from the surface, assist in maintaining the temperature of the body. Epidermis absorbs water with great rapidity, except where it is covered by a thin layer of oily matter. The osmotic properties of epithelium will be referred to in treating of osmosis in general.

2. VITAL PROPERTIES OF EPITHELIUM.

The nutrition of an epithelial layer depends upon the transudation of nutrient fluid from the bloodvessels underneath the layer of cells. It is usually very active, except perhaps in stratified epithelium. Most epithelial cells are constantly engaged in the formation of particular proximate principles. This is especially true of spheroidal epithelium, in the cells of which various substances, such as ptyaline, pepsine, &c., are formed. In some epithelial cells chemical transformations apparently take place. Thus, the superficial layers of the epidermis undergo changes which so alter the cells as to render them insusceptible of the action of acetic acid, while, in the deeper cells of the same layer, pigment may be formed. The exact mode of development of epithelial cells is still unknown, but there appears to be an incessant development of new cells from the surface of the membrane on which the deeper layer is situated. The new cells gradually pass outwards, and on reaching the superficial layer, last for a certain time and then drop off. This process of desquammation, as already stated, is preceded by chemical transformation. There is thus a constant elimination from the body of the materials which form epithelial cells.

Epithelial tissue is not sensitive, but in the structure of the terminal organs of sense epithelial cells may be modified for special purposes, as will be illustrated in treating of these organs.

3. Influence of Epithelium in Absorption and Elimination.

The function of epithelium in the process of absorption, or the introduction of matter from the external medium into the fluids or tissues of the body, may be briefly stated as follows :—

1. *Absorption of Gases and Volatile Substances.*—The pulmonary surface in the ultimate air cells of the lung, which is covered by a thin layer of flattened epithelial cells, absorbs oxygen and volatile matters. The surface of the skin, and perhaps also the intestinal mucous surface, absorb small quantities of gases.

2. *Absorption of Fluids and Soluble Substances.*—All epithelial surfaces may absorb water, or solutions of salts or other substances, but there are great differences in this respect. Thus, the pulmonary mucous membrane absorbs water freely; the epithelial lining of the bladder scarcely absorbs it at all ; while the intestinal mucous membrane permits readily the passage of water and of soluble matters. In certain circumstances, also, the epidermis covering the skin may permit the absorption of water.

3. *Absorption of Fat.*—The cylindrical or columnar epithelium of the lining of the small intestine absorbs fat by a process the mechanism of which will be described in treating of absorption.

4. *Influence of Epithelium in Elimination.*—The elimination of matters from the body may take place either by exhalation of watery vapour, of various gases, or of volatile substances, from epithelial surfaces, or by a true process of secretion, in which the spheroidal epithelial cells lining the ultimate pouches of glands constitute the active agents. Details regarding these processes will be given in treating of the functions of respiration and of secretion. In the meantime it is sufficient to state that the process of secretion is a distinct mode of activity of glandular epithelium.

4. Ciliated Epithelium and its Vibratory Motion.

Epithelial cells, on which cilia are placed, are generally of the columnar, sometimes of the spheroidal, rarely of the flat kind. These bodies constitute minute hair-like processes, attached to, or forming a prolongation of, the wall of the cell at its free side, and when covered with fluid, are in constant vibratory motion.

Ciliated epithelial cells do not differ materially from other cells of the same form, excepting in the possession of the cilia; they usually contain distinct nuclei; and they appear to be abraded from the surfaces on which they are situated, and to be replaced by successive layers of new cells, formed from the subjacent texture, and subsequently acquiring the ciliated structure when they reach the surface.

The number of cilia attached to each cell is subject to considerable variety. In some instances, only one or two, in others, a crown or circle of numerous cilia occupy the free surface of the cells.

The individual cilia are, in the human subject, generally from $\frac{1}{3000}$ to $\frac{1}{6000}$ of an inch in length; in invertebrata, they are often considerably longer. They are also proportionately thicker and blunter in vertebrate than in invertebrate animals.

Ciliated epithelium occurs in the human body in the following situations :—1st, on the mucous membrane of the air-passages, and the various sinuses and tubes communicating immediately with them—as in the nares (excepting close to their external openings) ; part of the soft palate, upper and lateral part of the pharynx, Eustachian tube, frontal, maxillary, sphenoidal, and ethmoidal sinuses ; on the conjunctiva palpebrarum, lachrymal sacs and nasal ducts ; on the mucous lining of the larynx, trachea, and bronchia, as far as their fine subdivisions, but not extending into the air-cells of the lungs : 2nd, in the adult female, the epithelium is ciliated in the lining membrane of the uterus, Fallopian tubes, and their fimbriated margins : and, 3rd, in the membrane lining the ventricles of the brain, the cells have been observed to be of a ciliated kind.

The movement of each cilium is most commonly of a folding or lashing kind. That of the whole set of cilia, covering a membranous surface, shows the passage of successive waves, somewhat in the same manner as different parts of the crop in a field of wheat are repeatedly bent in succession by the wind passing over it. When the ciliary motion is active, the movement is so rapid that the optical effect is the appearance of a stream of fluid flowing along the surface. This is the case especially when we look at a marginal line of cilia, as in the gills of a common mussel.

Four varieties of ciliary motion may be noticed :—(1) the *hook-like*, in which each cilium makes the movement of a finger which is alternately bent and extended ; (2) the *funnel-shaped*, in which the upper portion of the hair describes a circle in swinging, and the whole a cone, whose apex is formed by the firmly attached base of the cilium ; (3) the *oscillating*, in which the whole hair sways more like a pendulum, from side to side ; and (4) the *undulating*, when the hair executes a movement like the lash of a whip moderately wielded, or the tail of a spermatozoon. Of all these forms of ciliary motion, the first appears to be by far the most frequent. (Frey).

Ciliary movement is independent, so far as mere movement is concerned, of the circulatory and nervous systems; although, no doubt, its nutrition must be affected by these. Elevation of temperature up to about 40° C. increases the movement, when it ceases, probably from coagulation of the protoplasm in the cilia. Cold retards the movement. All substances having a chemical action on protoplasm, if applied in solutions of sufficient strength, stop ciliary action. Thus, water accelerates the movement at first, but soon stops it, probably by acting on the protoplasm. As a rule, fresh water stops ciliary motion in parts removed from inhabitants of salt water. Bile, acids, alkalies, and alcohol, if of sufficient strength, stop ciliary action; but, if in weak solutions, they may accelerate the movement. Ciliary movement requires the presence of oxygen, while the presence of carbonic acid seems to have a retarding influence. Cilia may be arrested by the action of chloroform or ether, and it is interesting to observe that they may recover from the influence of these substances. Electricity, whether applied as a continuous current, or from an induction coil, produces no appreciable effect.

Ciliary movement continues for a short time in small detached portions of the texture, and for a longer period in the entire part, after the destruction of the brain and spinal marrow, or after the first invasion of apparent death. The time of this persistence varies from a few hours to several days, in man and warm-blooded animals, and is even considerably longer in cold-blooded reptiles; it is much influenced by temperature, the nature of the fluids in contact with the texture, and other circumstances.

Various theories have been advanced to explain the action of cilia. Thus it has been supposed that each cilium is moved by two minute muscles inserted into its base (Ehrenberg); that it consists of a double spiral, which is continually winding and unwinding itself (Barry); that it is owing to imbibition of nutrient fluids (Beale); and that it is due to two contractile motions of unequal length—upon a longer one, produced by the contractility of the protoplasm, and a shorter one, caused by elasticity (Engelmann). It is most probable that it depends upon a phase of contractility in the individual cilium not yet understood.

Consult QUAIN'S Anatomy, p. 46. FREY'S Histology, p. 137. CH. ROBIN: Des Eléments Anatomiques et des Epithéliums, 1867. E. CABADÉ: Essai sur la Physiologie des Épithéliums, 1867. L. RANVIER: Art. Epithélium du Nouveau Dict. de Med. et de Chir. pratiques, t. XIII. As to ciliary motion, see article "Cilia," by SHARPEY, in Cyclop. of Anat. and Phys.; in QUAIN; and FREY'S Histology, p. 158.

IV.—THE CONTRACTILE TISSUES.

The phenomenon of contractility is exhibited by various cells, such as the colourless corpuscles of the blood, connective tissue corpuscles, the corpuscles of lymph, and the corpuscles of pus. These amæboid cells, when examined with sufficiently high power, manifest a slow circulation of the granules lying in the protoplasm, and also slow changes of form, such as have been already described in treating of that substance. They have been seen to take up into their substance small particles of pigment, such as carmine, indigo, and aniline, and even globules of milk, in the same manner as the actions of an amæba from a road-side pool. It has also recently been discovered that, by amæboid movements, contractile bodies may wander through the interstices of the tissues, a phenomenon termed the *migration of cells*, which is now regarded as important in such pathological processes as inflammation. The principal facts relating to the functions of such structures will be described under the head of animal movement, blood, and lymph. Here we shall discuss the properties of muscular fibre, which is the chief contractile tissue of the body.

There are two varieties of muscular tissue, namely, (1) The voluntary; and (2) The involuntary. The first of these consists of fibres, which always present the structural character of being marked with fine close cross-lines, or they are *striated;* in the second, for the most part, this appearance is wanting, or they constitute the *non-striated* form of muscular fibre. Some involuntary muscular fibres, however, as those forming the heart, part of the gullet, &c., being striated, are exceptions to this general statement.

A.—STRIATED MUSCULAR FIBRE.

1. Structure of Striated or Voluntary Muscular Fibre.

In any of the muscles of the limbs, or trunk of the body, the structure is somewhat complex. The muscular substance forms an elongated mass composed of bundles of fibres, the individual fibres and associated bundles being united together by layers of white fibrous tissue. The ends of the muscle are in general fixed to the places of their attachment by tendons, which in some cover, and in others mix with, the muscular bundles to a greater or less degree, and the whole is permeated by bloodvessels, lymphatics, nerves, fat, &c.

The *fasciculi*, or larger bundles visible to the naked eye, run parallel to each other in a voluntary muscle, and in each fasciculus the fibres run for a distance of 1½ inch. In some muscles the direction of the bundles corresponds with the length of the whole muscle, or the line between its opposite attachments; but this is not always the case, for the fasciculi and fibres not unfrequently run obliquely across the muscle, either in a single or a double series, as in the penniform or semi-penniform mode of arrangement. The fasciculi are of very various sizes, and the larger may be divided into smaller ones.

Each fasciculus may be separated into *fibres* of a determinate size, either by minute dissection, or by means of prolonged boiling, or by immersion for a time in weak acids, which dissolves the uniting connective texture without breaking up the muscular fibres. These fibres vary somewhat in size; the average may be stated at about $\frac{1}{400}$ of an inch in breadth, or $\frac{1}{350}$ in the adult male, and $\frac{1}{450}$ in the female. When united in fasciculi, they are of a prismatic shape in consequence of mutual compression. Each fibre is enclosed in a delicate homogeneous sheath named the *sarcolemma*, and by careful teasing with sharp needles, the fibre may be split up into fine longitudinal *fibrillæ*. The fibrillæ are composed of a semi-fluid matter, uniting a series of disc-shaped particles, known as *sarcous elements*. The separation of a muscular fibre into fibrillæ may sometimes be seen on breaking up the extremity of a fresh fibre by compression, and occasionally also by spontaneous separation in muscular fibre that has been preserved in chromic acid solutions or in weak alcohol. In other instances, muscular fibre that has been preserved shows a disposition to break in a different manner into transverse discs, the thickness of which corresponds with the distance between the transverse striæ and the sarcous particles; each disc consisting of the adjoining sarcous particles laterally united. The sarcolemma also, occasionally, becomes more obvious by the breaking up of the sarcous matter within it into distinct portions, between which the folded and contracted tube of sarcolemma may be perceived; and it is also sometimes seen raised from the sides of the sarcous mass by the imbibition of the water in which it may have been subjected to examination. Oval or flattened nuclei are frequently seen on the inner surface of the sarcolemma in mammalia, and dispersed through the thickness of the muscular fibres in the muscles of frogs, when their substance has been rendered transparent by the action of dilute acetic acid.

Recent researches made with high powers have shown that the structure of a muscular fibril is still more complex, the minute details of which may be found in histological text-books. Here it is sufficient to state that a muscular fibre consists (1) of a substance which forms the sarcous elements, highly refracting, and black when seen by transmitted light; and (2) of an intermediate or fundamental substance, which is much less refractive, and is clear by transmitted light. When examined with a Nicol's prism, the sarcous elements are found to be *anisotropic* or doubly refractive, while the substance which unites the contiguous discs is *isotropic*, that is, singly refractive, and according to Engelmann, contractility is manifested exclusively in the anisotropic portion. Each sarcous element behaves as a doubly refractive body having only one positive axis,[1] of which the optical axis is parallel to the long axis of the muscle. As they change their form during contraction, becoming shorter and thicker, they cannot be regarded simply as double refractive bodies, like crystals, but, as suggested by Brücke, they must consist of a great number of small doubly refractive particles, to which he has

---

[1] A body having its molecules uniformly arranged in all directions affects light only by *simple refraction*, that is, the incident ray gives rise to one refracted ray, and the crystal possesses one refractive index. When, on the other hand, the molecular structure of a body possesses parts of different density in certain directions, it manifests double refraction, that is, a ray of light traversing it is divided into two rays, one of which is bent more out of its course than the other. Common glass is simply refractive, and is said to be *isotropic*; but if it be compressed in one direction, it may become doubly refractive or *anisotropic*.

given the name of *disdiaclasts*, and which he supposes are irregularly distributed through the fundamental substance. The latter, which may be termed *muscle-plasma*, is a viscous liquid capable of absorbing water freely, while the disdiaclasts are more dense and are less capable of taking up water. As has been remarked by Schäfer, Brücke himself pointed out that in living muscle at rest the whole of the muscular substance appears doubly refracting, and that it is only in contraction the alternate stripes appear singly refracting.—(Brücke's Physiologie, p. 465.)

The bloodvessels and nerves ramify in the connective tissue, which fills up the spaces between the larger and smaller fasciculi. The smallest bloodvessels form a fine network of long shaped meshes between the fibres, but not extending within the sarcolemma.

The connection of muscular with nervous fibres may be of the following nature: (1) According to Kühne, the nerve filaments perforate the sarcolemma, and terminate in the interior of the fibre in a finely granular mass of matter, which may be called an *end-plate.* (2) Beale, Kölliker, Krause, and others have, on the other hand, described the nerve fibres as terminating in a *plexus* distributed on the external surface of the sarcolemma. According to these authorities, the ultimate nerve fibrils never penetrate the muscular fibre. This point still requires further investigation, but the evidence is in favour of the view that the ultimate nervous filaments end in plates, which, whether they are situated within, or outside the sarcolemma, may be regarded as the *motor terminal organs.*

The voluntary muscles are striated in all the vertebrate and articulate animals, they are partially so in several classes of echinoderms, but generally not striated in mollusca. The size of the entire fibres does not appear to be proportional to that of the sarcous particles as measured by the distance between the transverse striæ. The fibres are of the smallest size, and consequently the bloodvessels are most finely distributed in those animals in which the contractility is greatest.

The following table gives certain measurements of muscular fibres in fractions of an inch:— (*Allen Thomson.*)

MUSCLE OF	DIAMETER OF FIBRES.			DISTANCE OF TRANSVERSE STRIÆ.
	Greatest.	Least.	Average.	
Birds, ...	$\frac{1}{350}$	$\frac{1}{1500}$	$\frac{1}{810}$	$\frac{1}{10400}$
Mammalia,......	$\frac{1}{192}$	$\frac{1}{1100}$	$\frac{1}{560}$	$\frac{1}{10900}$
Man,.............	$\frac{1}{192}$	$\frac{1}{615}$	$\frac{1}{400}$	$\frac{1}{9400}$
Reptiles,.........	$\frac{1}{100}$	$\frac{1}{1000}$	$\frac{1}{480}$	$\frac{1}{11500}$
Fishes,...........	$\frac{1}{65}$	$\frac{1}{755}$	$\frac{1}{220}$	$\frac{1}{11100}$
Insects,..........	$\frac{1}{200}$	$\frac{1}{755}$	$\frac{1}{420}$	$\frac{1}{9500}$

Regarding the structure of muscular fibre, see QUAIN'S Anatomy, p. 108; SCHÄFER'S Practical Histology; Phil. Trans. 1873. The Original Researches on Muscle, by BOWMAN, will be found in Trans. Roy. Soc. London, 1840, and Art. Muscle in Cyclop. of Anat. and Physiol.; TODD and BOWMAN'S Anat. and Phys. See also DOBIE, Annals of Natural History, Feb. 1848. Regarding the optical properties of muscle, consult BRÜCKE, Denkschriften d. Wiener Akademie, 1858; SCHULTZE, Archiv. f. Anat. u. Physiol., 1861; HÄCKEL, *ibid.*, 1857; and SCHÄFER'S Practical Histology.

2. CHEMISTRY OF MUSCULAR FIBRE.

Muscular fibre is composed of two parts—(1) *muscle-plasma,* which may be separated by pressure from muscle removed from a recently-killed cold-blooded animal, as a neutral or slightly alkaline gelatinous fluid; and (2) *an insoluble residue*, consisting probably of sarcolemma, nuclei, fat, and matters derived from the vessels, nerves, and lymphatics mixed with the muscular tissue. Nothing is known regarding the chemical composition of the disdiaclasts as distinguished from the fundamental matter of the fibre. The *muscle-plasma* may be obtained by compression, at a low temperature, of muscles deprived of blood. It is an alkaline, colourless, or faintly yellow fluid, containing various albuminates. When obtained pure, it speedily coagulates and separates into two portions—*muscle-clot* or *myosin* and *muscle-serum.* Coagulation is accelerated by heat, distilled water, weak acids, ammonia, &c., and it is retarded by cold. Myosin is an albuminous body, soluble in common salt or weak hydrochloric acid. Acids convert it into an allied substance named *syntonine*, which is not soluble in common salt or in a solution of sulphate of magnesia.

Muscle-serum contains the following substances:—

(1) *Albuminates*, such as albuminate of potash, which is precipitated on heating from 20° to 40° C., and by neutralizing the alkaline fluid. Ordinary albumen, such as is found in the serum of the blood, is precipitated when the fluid is rendered acid and heated up to 75° C.

(2) Traces of *animal ferments*, namely, pepsin and ptyaline.

(3) A *colouring matter*, which would appear to be identical with hæmoglobine, the colouring matter of the blood. As to its exact identity with that pigment, further research is necessary.

(4) Various *nitrogenous proximate principles*, all of which have been discovered in extract of meat—namely, creatine, creatinine, xanthine, hypoxanthine, taurine, urea, and inosic and uric acids.

(5) Various *non-nitrogenous proximate principles,* such as para- or sarco-lactic acid,[1] inosite or muscle sugar, glycogen or animal starch, dextrine, and glucose. Small quantities of volatile acids, such as formic, acetic, and butyric acids, have been found. In dead muscle, or in muscle which has been excited to frequent contractions in short intervals of time, lactic acid, or the variety called para- or sarco-lactic acid, has always been found, and it has been supposed to originate from the sugar or glycogen present in the muscle.

(6) The principal *salts* are the phosphates of the alkalies and alkaline earths, chloride of potassium, and a small quantity of chloride of sodium and of sulphates of the alkalies.

(7) *Water* forms about three parts of the weight of muscle.

(8) The following *gases* have been separated from 100 parts of muscle :—Carbonic acid, 14·40; nitrogen, 4·90; and oxygen, ·09—total, 19·39. It is probable that much of the carbonic acid may have arisen from decomposition.

---

[1] The difference between ordinary lactic acid, as obtained from milk or sugar, and paralactic acid, as obtained from flesh, is most distinctly marked in their calcium and zinc salts, the acids themselves being scarcely distinguishable. The calcic salt of paralactic acid contains 2 atoms of water of crystallization, while that of lactic acid contains 2½ atoms. Again, paralactate of zinc differs from lactate of zinc both as regards water of crystallization and solubility. The different structure of the two acids has been thus represented graphically :—

$$\left.\begin{array}{l} CH_3 \\ CHOH \\ COOH \end{array}\right\} \qquad \Bigg| \qquad \left.\begin{array}{l} CH_2OH \\ CH_2 \\ COOH \end{array}\right\}$$

Lactic. | Paralactic.

The empirical formula of both is $C_3H_6O_3$, but from their physical differences, no doubt the atoms or groups of atoms contained in them are differently arranged.

Von Bibra gives the following rough quantitative analysis of muscle from different species of animals in 1,000 parts:—

	Man.	Ox.	Bird.	Fish.	Frog.
Water,................	745·5	776·0	717·6	797·8	804·3
Solids,................	255·5	224·0	282·4	202·2	195·7
Albumen, ...	19·3	19·9	26·8	23·5	18·6
Gelatinous matter,..	20·7	19·8	12·3	19·8	24·8
Alcoholic extract,...	37·1	30·0	41·2	34·7	34·6
Fat, ...	23·0	—	25·3	11·1	1·0
Vessels, &c., ...	155·4	154·3	176·8	113·1	116·7

Fresh beef, on calcination, has yielded 1·46 to 1·63 per cent. of ash,—in 100 parts of which there are 35·94 of potassium; traces of sodium; 3·31 of magnesium; 1·73 of calcium; 4·86 of chlorine; ·98 of iron; 34·36 of phosphoric acid; 3·37 of sulphuric acid; 2·07 of silicic acid; and 8·02 of carbonic acid.

Glycogen or animal starch abounds in the muscles of the embryo and of the fœtus, and the muscles of young animals contain more water than those of animals advanced in age. The amount of fat also increases with age.

Living muscle in a state of rest, as already mentioned, is slightly alkaline from containing phosphate of potash, K_2HPO_4. After a period of activity it becomes acid, partly by the formation of free lactic acid from carbo-hydrates, and, according to some authorities, partly from the presence of the acid phosphate of soda, KH_2PO_4.

Consult Beaunis' Physiologie, p. 172; Wundt's Physiologie, p. 372; Kühne, Physiolog. Chemie.; Art. Muscular Tissue, in Watt's Dictionary of Chemistry.

3. PHYSIOLOGICAL METHODS OF STUDYING MUSCLE.

Before entering upon the study of the properties of muscle, it will assist the student to describe briefly the methods now adopted by physiologists in investigating the phenomena of muscular and nervous action. At the same time he should remember that it is of far more importance to be acquainted with the results than with the methods by which these have been obtained; but knowledge can only be definite and complete where there is an intelligent appreciation of both.

1. *Measurement of Short Intervals of Time.*—As many of the phenomena of nervous and muscular actions are of such short duration as to make it impossible to observe their phases with the unaided senses, it is necessary to construct apparatus for the measurement of minute intervals of time. Accordingly, in recent years, much ingenuity has been expended in the construction of chronographic or time-measuring instruments, of which the following are examples:—

a. Recording Cylinder.—This is a cylinder revolving at a uniform rate by means of clockwork. Suppose the surface of the cylinder to be divided by sixty lines, parallel with its axis, at equal distances from each other, and that the cylinder makes one revolution in a second, the distance between two of the lines will represent the $\frac{1}{60}$th part of a second, and any phenomenon recorded on the moving cylinder between the two lines must have happened during that interval of time. It is evident that by means of such an arrangement, seen in Fig. 1, first suggested by Thomas Young, intervals of time, even to the fraction of $\frac{1}{1000}$th of a second, may be measured with accuracy. The principal difficulty in such graphic measures of time is to have the cylinder revolving at a uniform rate. This is accomplished by means of regulators, of which the simplest is that of Foucault, now attached to all revolving cylinders used for physiological purposes. To obtain, on a revolving cylinder (the time occupied by a revolution of which is not known), continuous registration of minute intervals of time, it is necessary to make use of a chronograph.

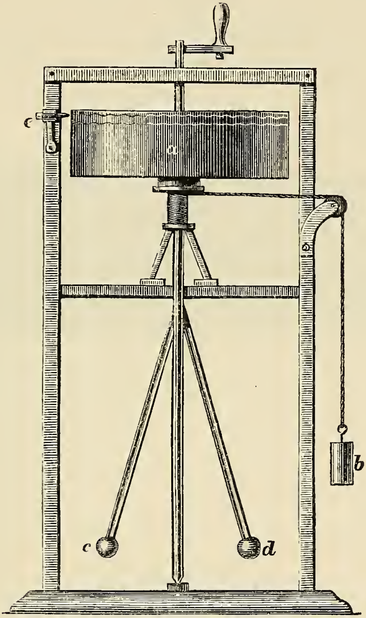


Fig. 1.—Original chronometer devised by Thomas Young for measuring minute portions of time: *a*, cylinder revolving on vertical axis; *b*, weight acting as motive power; *c d*, small balls for regulating the velocity of the cylinder; *e*, marker recording a line on cylinder. This fig. is introduced as showing the first apparatus designed for chronographic tracings. See Young's Lectures on Natural Philosophy, Lect. XVII., On Time-keepers, plate xv., fig. 198.

b. Chronographs.—Thomas Young was also the first to devise the method of inscribing upon a rotating cylinder all the vibrations of a metallic rod bearing a very light style or marker. When these vibrations are isochronous, each of the undulations traced upon the cylinder corresponds to a regular interval of time. Duhamel was the first to apply to one of the limbs of a tuning-fork a small marker, which traces with great regularity the vibrations of the tuning-fork, and in this way, if the surface receiving the tracing be moving with sufficient rapidity, intervals of the $\frac{1}{500}$th of a second, or less, may be readily measured. An example of tracings thus obtained is seen in Fig. 2.

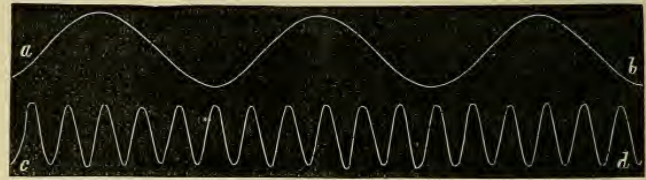


FIG. 2.—Tracings of a recording tuning-fork, ten vibrations per second; *a b*, cylinder moving rapidly; *c d*, cylinder moving slowly.

Marey, the distinguished professor of experimental physiology in the College of France, who has done more to advance the graphic method of recording physiological phenomena than any man living, has devised an apparatus which consists of a marker vibrating in unison with a tuning-fork kept in action by interruptions of an electric current. The apparatus, as applied to a revolving cylinder, is seen in Fig. 3.

It consists of three distinct parts—a battery, an interrupting tuning-fork, and the chronograph. This last piece of apparatus, seen in Figs. 4 and 5, consists of a very fine stylet fixed at the extremity of a steel plate, and armed with a small mass of steel, somewhat wedge-shaped, which fits in between two small keepers, *b b*, of the electro-magnets, *a a*.

The tuning fork merely interrupts the current from the battery. This it does automatically. When the electro-magnet between the limbs of the tuning fork is magnetic, the limbs are, of course, approximated, and a small piece of platinum wire affixed to one of them is removed from contact with a platinum surface (Fig. 3, *i*), so as to break the circuit. On the circuit being thus broken, the electro-

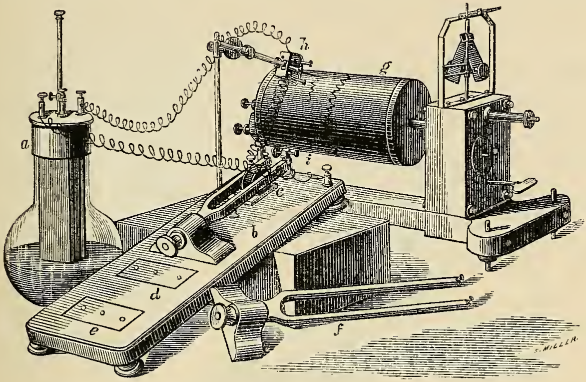


Fig. 3.—Marey's chronograph as applied to revolving cylinder. *a*, galvanic element; *b*, wooden stand bearing tuning-fork (200 vibrations per second); *c*, electro-magnet between limbs of tuning-fork; *d e*, positions for tuning-forks of 100 and 50 vibrations per second; *f*, tuning-fork lying loose, which may be applied to *d*; *g*, revolving cylinder; *h*, electric chronograph kept in vibration synchronous with the tuning-fork interrupter. The current working the electro-magnet from *a* is interrupted at *i*. Foucault's regulator is seen over the clock-work of the cylinder a little to the right of *g*.

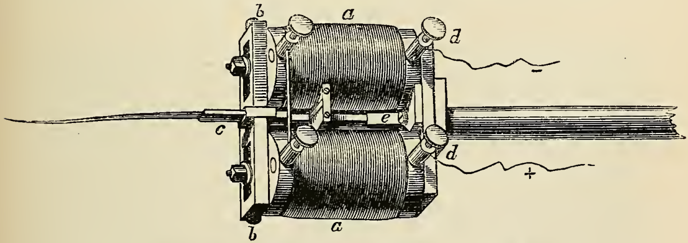


Fig. 4.—Side-view of Marey's chronograph. *a a*, coils of wire; *b b*, keepers of electro-magnets; *c*, vibrating style fixed to the steel plate *e*; *d*, binding screws for attachment of wires; + from interrupting tuning-fork; — to the battery.

magnet ceases to act, the limbs of the tuning fork recede from it, so as again to bring the platinum wire in contact with the platinum surface, and thus again to complete the circuit. The chronograph, as already explained, vibrates in unison with the tuning fork. The great advantage of this apparatus is its accuracy and facility of ready adjustment, and it can frequently be applied where it would be extremely difficult to bring the tuning fork into direct contact with the moving surface.

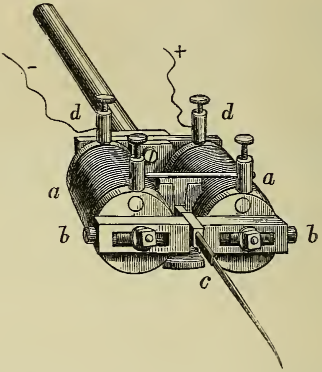


Fig. 5.—Perspective view of Marey's chronograph, intended to show the position of the vibrating style. Same description as for Fig. 4.

c. *Electrical Signals.*—It is often of great importance to determine the moment of the commencement or termination of a phenomenon. This is readily done by means of electro-magnetic arrangements, such as is seen in Fig. 6.

The apparatus consists of two electro-magnetic bobbins, which, the moment the current passes, attract a steel plate placed above them, and draw down the writing stylet, so as to make a lower horizontal line. When the current is interrupted, the spiral spring elevates the lever, which traces an upper horizontal line until the current is again closed. The current may be opened or closed by means of a pendulum, or a tuning fork, or by a metronome. By such an arrangement of closing or of opening the circuit, the instant

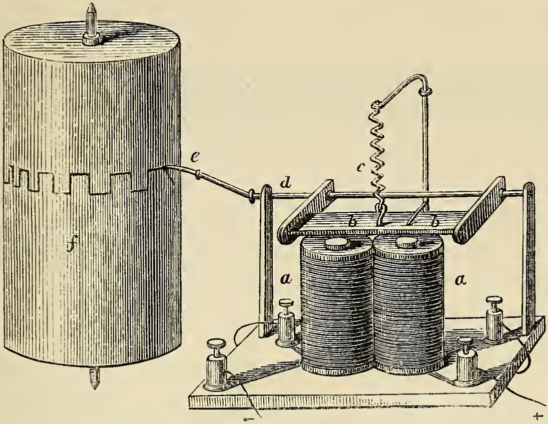


Fig. 6.—Apparatus for writing electro-magnetic signals upon a revolving cylinder; *aa*, bobbins covered with wire; *b*, steel plate fixed in a frame, which is pulled downwards when the iron cores of the bobbins become magnetic; *c*, steel spring, by the elasticity of which the plate is drawn quickly upwards when released from the bobbins; *d*, rod bearing stylet, which is marking upon the cylinder *f* at *e*. (*Marey.*)

of the commencement or termination of any phenomenon will be recorded. An example of a tracing obtained by such an apparatus is given in Fig. 7.

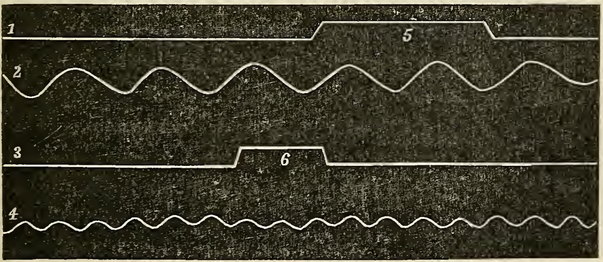


Fig. 7.—*1*, Line marked by stylet; *2*, vibrations of tuning fork—10 vibrations per second; *5*, electric signal—the rise in the tracing of *1* indicates the interruption, and the fall the formation of the current. Cylinder revolving with great rapidity. *3*, *4*, and *6* show similar tracings, with the cylinder moving slowly. (*Marey*).

A small instrument similar to Marey's chronograph, and on the same principle, has been invented by Deprès, and is of such extreme delicacy as to record electrical signals at a rate of from 700 to 800 per second.

FIG. 8.—Signals obtained by the apparatus of Deprès, acted upon by an interrupting tuning fork of 500 vibrations per second. (*Marey.*)

2. *Instruments for recording Muscular Contraction.*—By the term *myography* is meant the study of muscular contraction by the aid of registering apparatuses. The muscle

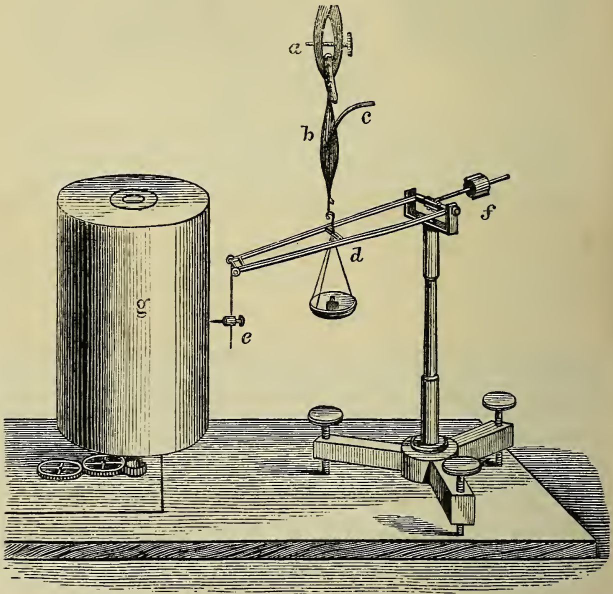


FIG. 9.—Myograph of Helmholtz. *a*, forceps for holding femur of frog; *b*, gastrocnemius muscle; *c*, sciatic nerve; *d*, pan for weights; *e*, stylet for recording on cylinder *g*; *f*, counterpoise by moving which the weight of the framework may be reduced to a minimum. The clock work is diagrammatic.

in contracting is caused to inscribe upon a surface the curve of its movement. The movement of a muscle may be divided into two secondary movements, namely, a shortening or contraction, and a thickening or increase in diameter. The first myograph, invented by Helmholtz, consists of a brass framework, Fig. 9, moveable round a horizontal axis, and kept in equilibrium by a counter-weight. The tendon of the muscle is fixed by a hook to the middle of the frame, and a balance for the purpose of carrying weights is attached underneath. At the other extremity of the axis of rotation, the frame carries a stylet, which traces the movements of ascent or of descent of the muscle upon any surface. The registering surface may consist either of a stationary plate of smoked glass, as in the arrangement of Fick, or of a vertical rotating cylinder (Fig. 9). When the tracing is obtained by Fick's method, it consists of a series of vertical lines, as seen in Fig. 10.

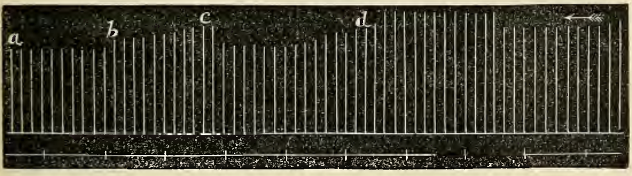


FIG. 10.—Example of myographic tracing, obtained by the method of Fick.

An extremely convenient form of myograph for physiological purposes is the spring myograph of Du Bois-Reymond, seen in Fig. 11.

This consists of a rectangular glass plate, *b*, moving horizontally between two slender steel wires, *d*. It may be impelled horizontally by the recoil of a steel spring, *c*, when a check is set free at the other end of the apparatus. Thus applied, the muscular contraction will produce a curve.

By removing the rod carrying the steel spring, the smoked glass plate may be slowly moved in front of the stylet by means of a long screw attached to the plate, the handle of which is seen a little below *c*.

In Helmholtz and Fick's arrangement, whether applied to a cylinder or to a moving glass plate, the muscle must be placed in a vertical position and have a certain weight to bear. Nor can the apparatus be conveniently applied to the muscle while *in situ* in the body of the animal recently killed. There is thus a want of sensitiveness and a want of convenience, both of which are to a great extent obviated by the myograph of Marey. The arrangement of this apparatus is seen in Fig. 12.

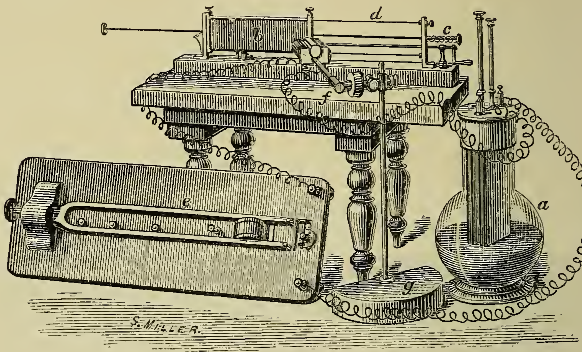


FIG. 11.—Spring myograph, showing Marey's chronograph applied to it for the purpose of ascertaining the velocity with which the blackened glass plate *b* is drawn across by the recoil of the spring *c*.

The principal piece of the apparatus consists of a horizontal brass plate supporting the axis of a registering lever, which moves in a horizontal plane. Consequently the lever registers upon a cylinder moving horizontally. A thread attached to the tendon of the gastrocnemius muscle of a frog is fixed by a small button to the lever. Fixed to the brass plate, and upon the same plane, there is a flat piece of cork on which the pithed or decapitated frog is laid.

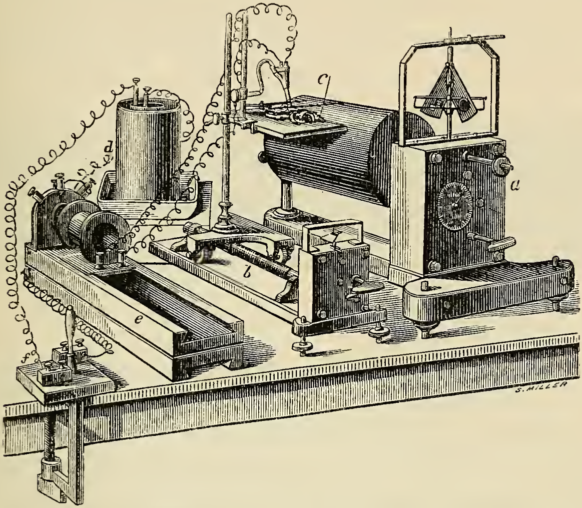


Fig. 12.—Arrangement of apparatus for experiment with the myograph of Marey: *a*, recording cylinder; *b*, railroad carrying the myograph *c*; *d*, galvanic element; *e*, induction coil; *f*, key.

A diagrammatic view of the apparatus is shown in Fig. 13. Attached to the side of the cork plate, there is a brass support bearing the electrodes for stimulating the nerve or muscle. When the muscle is stimulated electrically, it contracts and moves the horizontal lever, which traces a curve upon the moving cylinder. If it be desirable to have a series of tracings from a muscle for a considerable period of time, these may be obtained by placing the entire apparatus upon a support, moved by clockwork upon a little railroad, parallel with the

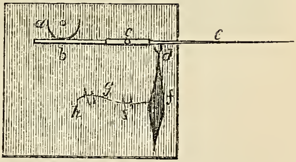


Fig. 13.—Diagram of the frog-plate of Marey's myograph: *a b*, *c e*, registering lever having fulcrum at *a*, and power at *d*, where the tendon of the muscle *f* is attached; *g*, nerve lying across wires represented by the lines *h* and *i*.

registering cylinder. Marey has also devised a double myograph, which differs from that just described only by having a second lever, so that the two gastrocnemei of a frog may be attached each to a lever; the two levers are superposed, and the tracings are close together but still distinct. By such an arrangement it is possible to study graphically the forms of the curves obtained by the contractions of two muscles under different conditions, say the one poisoned and the other normal.

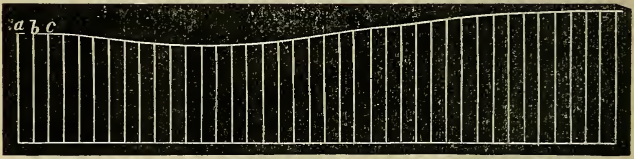


FIG. 14.—Myographic tracing obtained by the method of Fick: changes in the amplitude of contractions of a muscle under the influence of a gradually increasing temperature. To be read from left to right.

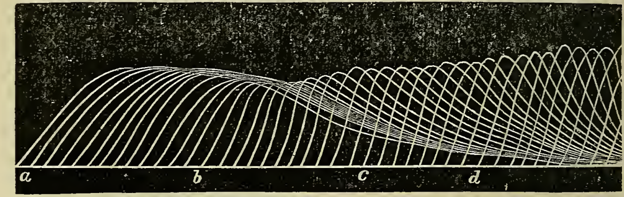


FIG. 15.—Myographic tracing obtained by the method of Marey, corresponding to a gradual heating of a muscle, as in Fig. 14 It will be noticed that not only does the amplitude of the contractions change, but also their form and their duration. To be read from left to right.

The great advantage of Marey's method is that it registers the curve of muscular contraction so as to give its different phases of movement, This will be appreciated upon comparing the two tracings seen in Figs. 14 and 15, which show the changes in muscular contraction under the influence of a gradually increasing temperature. (*Marey.*) It may be observed in both that the rise of temperature increases the amplitude of the contraction, but the vertical lines do not indicate whether or not any change has taken place in the duration of the contraction. It will be seen, however, in studying Fig. 15, that heat not only changes the amplitude, but causes the contraction and relaxation to occur in shorter intervals of time.

3. *Apparatus required for Electrical Stimulation of Muscle.*—The galvanic elements usually employed are Smee's or Daniel's elements. For induction currents, the form of apparatus known as Du Bois-Reymond's electro-motor is the most convenient. This apparatus is shown in Fig. 16. It

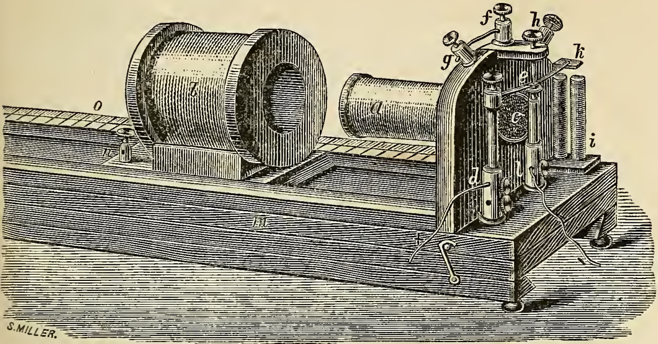


FIG. 16.—Electro-motor of Du Bois-Reymond: *a*, primary coil; *b*, secondary coil; *c*, bunch of wires in centre of primary coil, for increasing intensity of induction current; *d*, binding screw, for attachment of wire from galvanic element. The current passes up the pillar *d*, along steel spring to *e*, from there to the screw *h*, the point of which touches the back of the spring at *e*. From *f* to *g*, thence through wire of primary coil to *i*, along the two pillars of soft iron *i*, which it renders magnetic and thus draws down the head of the spring *k*. This interrupts the current at *e*, by breaking the contact of the spring with the screw point. When the current is thus interrupted, the spring flies up by its elasticity and again forms the current at *e*. Thus the current is broken and formed automatically, and each time it is broken and formed there is an induction shock from the secondary coil *b*. The intensity of the induced current becomes weaker as we withdraw *a* from *b* along the graduated board *o*. The automatic apparatus was devised by Neef. When the wires from the battery are connected with *g* and *h*, Neef's arrangement is out of the circuit, and an opening or closing shock may then be obtained by opening or closing a key (Fig. 17, VI.) interposed in the circuit.

is not within the scope of this work to describe minutely various forms of apparatus used in electro-physiology; but to assist the student in identifying them when studying their practical applications, a group of these is shown in Fig. 17.

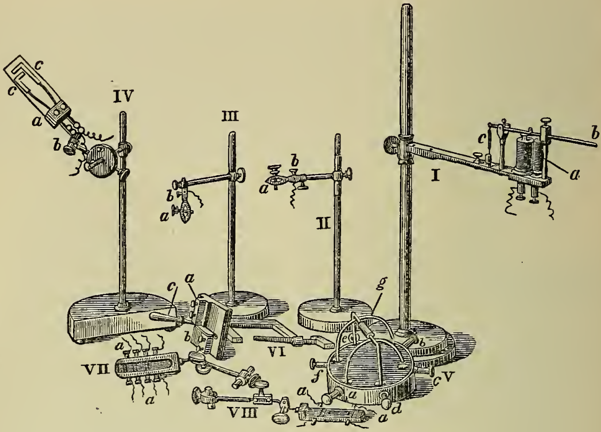


Fig. 17.—Apparatus for electrical experiments on muscle and nerve. I. Electro-magnetic signalling apparatus, for recording seconds on a revolving cylinder; *a*, bobbins covered with wire; *b*, brass rod carrying pencil or pen; *c*, steel spring. II. and III. Brass forceps for holding leg of frog; *a*, forceps; *b*, binding screw for wire. IV. Platinum electrodes for stimulating nerve; *a*, piece of vulcanite carrying glass plate, *c c*, on which are the copper wires terminating in rectangular platinum points; *b*, universal joint. V. Pohl's commutator for reversing the direction of electric currents; *d*, and *e*, are connected with the battery or induction coil; *b c*, and *a f*, are binding screws for attaching wires in different circuits; *g*, bridge of copper wire, divided and insulated in the centre by glass tube, for the purpose of sending the current entering by *d e*, either in the direction of *b c*, or *a f*. VI. Du Bois-Reymond's key, consisting of a piece of vulcanite on which there are two rectangular pieces of brass, *a b*, each having two binding screws. The two pieces of brass are connected by an arm of brass, the handle of which is seen at *c*. VII. and VIII. Two forms of apparatus for stimulating nerve, consisting of vulcanite troughs, into which are fixed platinum wires, which may be attached to the wires coming from the battery by binding screws at *a a a a*.

Consult Foster, in Hand Book for the Physiological Laboratory, p. 341 *et seq.*; Articles on La Méthode Graphique dans les Sciences Experimentales, in Marey's Physiologie Expérimentale, 1875-76; also, the Author's Lectures on the Graphic Method before the

Faculty of Physicians and Surgeons in Glasgow, 1877. For elaborate details see GSCHEIDLEN'S Physiologische Methodik, and CYON'S Practische Physiologische.

4. GENERAL PHYSICAL PROPERTIES OF MUSCLE.

1. *Consistence.*—When a muscle is in the contracted condition, it is hard and resistant, and when it is relaxed it is soft. In the state of rigidity which follows death, muscle becomes firm and solid.

2. *Cohesion.*—The cohesion of muscular tissue is much more feeble than that of the connective tissues, and especially than that of tendon. The cohesion of muscular tissue exerts an influence during pressure and traction. The resistance to traction is influenced by the state of the muscle; according to E. Weber, a square centimetre of frog's muscle may support a weight of a kilogramme without rupture. The disappearance of muscular irritability is accompanied by a diminution of cohesion. Thus the gastrocnemius of a dead frog, which has lost all its irritability, will break with a weight of about 260 grammes, while a similar muscle from a frog just killed will carry without rupture a weight of 1½ kilogrammes.

3. *Elasticity.*—The elasticity of living muscle is small, but nearly perfect; that is, the muscle will elongate easily under the influence of very small weights, and will return on their removal exactly to its former length. The elasticity of muscle may be readily studied by means of Helmholtz and Fick's modification of the myograph, by which the amount of stretching by different weights, placed in a pan, may be readily measured. It will then be seen that the elongations of the muscle are not exactly proportional to the weights which stretch it. The proportion of the elongation diminishes as the weights increase, so that the curve of

muscular elasticity approaches that of a hyperbola, and is not a straight line. The limit of elasticity is considerable. It is difficult to state the limit, but it is known that the gastrocnemius of a frog, weighted with 100 grammes, will not return to its primitive length. According to Weber, the elasticity of an active muscle is diminished. He arrived at this result by tetanising the hyoglossus muscle of a frog securely fixed at one end and having weights attached to the other. He compared the amount of elongation during the state of contraction with elongations caused by the same weights upon the same muscle in repose. He found, for example, a greater elongation in the contracted muscle with one and two grammes than when it was produced by the same weights attached to the muscle in repose. He also made the following curious observation: if a muscle in repose be heavily weighted, and then stimulated, it may become longer instead of shorter; that is to say, the shortening due to contraction is not sufficient to compensate for the elongation due to diminution of the elasticity. Volkmann pointed out, after an elaborate research, in which he did not employ tetanic excitations, as Weber had done, but isolated opening induction shocks, that Weber had exaggerated the diminution of elasticity in active muscle, and that the results are largely affected by the condition of fatigue. Wundt has also arrived at results contrary to those of Weber. He adopted the method of arresting by an overweight the contraction of a muscle, and he found that the diminution of muscular elasticity does not depend upon the state of activity, but simply upon shortening of the muscle. He says, "if the diminution of elasticity depends upon the state of activity, it "would follow in my mode of experimenting, that at the "moment of excitation there ought to be an elongation of "the muscle, its elasticity having been diminished—a result "which never happens." He arrives at the general conclusion that the elasticity of active muscle is the same as that of muscle in repose. These results have been confirmed by the research of Donders and Van Mansveldt, conducted upon the flexor muscles of the fore-arm of man. To recapitulate: (1) the elongation of muscle is within certain limits proportional to the weight; (2) the coefficient of elasticity is very nearly the same for different degrees of contraction; and (3) fatigue diminishes elasticity.

The elasticity of muscle plays the important part of fusing together the numerous individual shortenings, which, as will be seen in studying muscle in the active condition, make up a single contraction. According to Marey, it favours the production of muscular work, in virtue of a law which he thus formulates: when a force of short duration is employed to move a mass, a more useful effect is obtained when it acts upon this mass through the intervention of an elastic body. The feeble elasticity of muscle is such as to oppose very little resistance to antagonist muscles, and when the contraction of the antagonist ceases, it restores the muscle to its natural length without loss of force.

4. *Tonicity.*—In the living being, muscles are more or less stretched between their two attachments. Thus they are in a state of tension or tonicity, sometimes termed *muscular tonus*, it may be by the contraction of antagonist muscles, or even by the elasticity of the skeleton or of the soft parts. When a muscle is divided transversely, or its tendon is cut, it therefore immediately contracts, and the two parts separate a certain distance from each other. The sphincters are the only muscles which, during repose, do not appear to be stretched. Their tonicity operates only when they are dilated.

Various controversies have arisen upon the question of whether or not muscular tonus is under the influence of the nervous system. Brondgeest divided in a frog the spinal cord below the medulla oblongata, and then divided the nerves of the leg on one side; on suspending the frog, he found that all the articulations of the leg of the operated side were loose and flaccid, and he concluded that the spinal cord furnished the flexors with permanent innervation. Heidenhain, on the other hand, found that when a muscle was placed in a certain degree of tension by a weight, it did not elongate after section of the nerve supplying it. The probability is that both innervation and the circulation of the blood have a certain influence upon muscular tonicity, by affecting the nutrition of the tissue.

Consult BEAUNIS' Physiologie, p. 255; WUNDT'S Physiologie, p. 374 and p. 427; ED. WEBER, art. Muskelbewegung dans Wagner's Handwörterbuch, t. III, 1846; Id. Ueber die Elasticität der Muskeln. (Arch. de Müller, 1858); VOLKMANN, Archiv f. Anat. u. Physiol., 1857 to 1860; WUNDT, Lehre von der Muskelbewegung, 1858; also MAREY, Rôle de l'Élasticité dans les Appareils Moteurs des Êtres Vivants. Physiologie experimentale, 1875.

5. ELECTRICAL PROPERTIES OF MUSCLE.[1]

a. *Apparatus.*—For the purpose of studying these properties, an extremely sensitive *galvanometer* is required, the most convenient being the reflecting galvanometer of Sir William Thomson, seen in Fig. 18.

This instrument is upon the same principle as the ordinary galvanometer, but it is modified by having the needles constituting the astatic system very short and very light, by having the coils of wire in the bobbins brought as close to the needles as possible, and by having a small silvered mirror attached to the uppermost group of needles. A lamp

---

[1] A short account of the discovery of animal electricity, and of its important relations to the progress of physical science, will be found in Appendix B.

is placed in front of the little mirror, and a ray of light is reflected by the mirror upon a scale placed at a convenient distance in front of the instrument. All of these arrangements secure extreme delicacy.

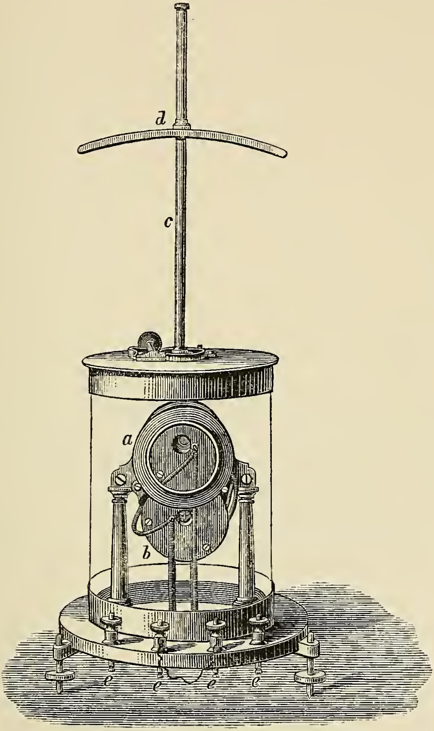


Fig. 18.—Reflecting galvanometer of Sir William Thomson—*a*, upper, and *b*, lower bobbin of fine wire ; a small mirror is attached to the upper group of magnetic needles in the centre of *a; c*, brass rod, bearing *d*, a curved magnet for regulating the position of the needles underneath ; *e e e e*, binding screws.

If metallic conductors, say composed of zinc, from the galvanometer, were brought into connection with a piece of living muscle, little or no current would be obtained, and even if there were a current it might be due to contact of the metallic conductors with the living tissue exciting electrolytic decomposition. Hence it is necessary to have a fluid interposed between the metal and the animal tissue, as, for example, the zinc wire or plate forming the terminals of the galvanometer must be immersed in a saturated solution of sulphate of zinc. But as sulphate of zinc solution would have the effect of irritating the living muscle, it is necessary to have an inactive substance between the tissue and the sulphate of zinc solution. All of these conditions are fulfilled by the arrangement of Du Bois-Reymond, which is that usually employed, and which may conveniently be termed the *non-polarizable electrodes.* Many modifications of this apparatus have, from time to time, been employed for particular purposes, but the form most convenient for demonstrating the principal electrical phenomena of nerve and muscle is what is here described. It consists (Fig. 19) of two troughs made of zinc, mounted on insulating plates of vulcanite. The inner surfaces of the troughs are carefully amalgamated, and they are filled nearly full of a saturated solution of sulphate of zinc. Into each trough is then placed a small cushion of clean blotting or filtering paper, which quickly becomes permeated by the solution. Finally, a small thin film or plate of sculptor's clay, or kaolin, moistened with a half per cent. solution of common salt, or still better, with saliva, is laid on each paper pad. These clay-pads are for guarding the tissue from the irritant action of the sulphate of zinc. Wires are conducted from the trough to the galvanometer, and it is convenient to have a key (Fig. 17, VI) interposed in the circuit, so that any current from the troughs may be permitted to pass to the galvanometer, or be shut off at pleasure. It is essential that no currents are derived from the troughs or from any of their connections, that is, to have the apparatus non-polarizable. This can only be done by taking extreme care in all the arrangements, and by connecting the troughs for a few hours before the experiment by a thick copper wire (passing from *f* to *f*) and laying a morsel of moist blotting paper from one paper cushion to the other so as to place the troughs in circuit.

The existence of currents from living muscle may also be demonstrated by what may be called the *galvanoscopic foot.*

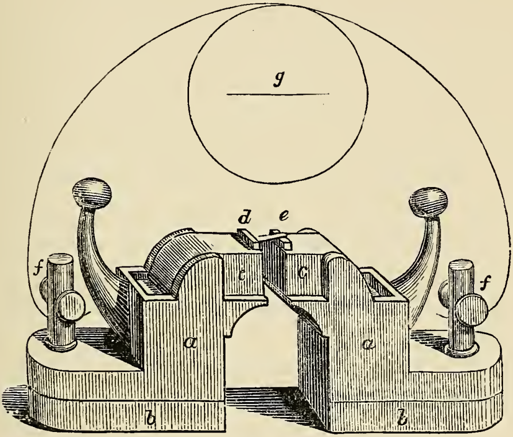


FIG. 19.—Diagram of apparatus of Du Bois-Reymond for experiments on the electrical condition of muscle and nerve: *a*, zinc troughs, mounted on pieces of vulcanite *b*; *c*, paper pads; *d*, *e*, small pieces of moist clay; *f*,*f*, binding screws for attaching the terminals of the galvanometer *g*. Observe a small bit of paper connecting *d* and *e*, and thus completing the galvanometer circuit. (*Wundt.*)

It is the leg of a frog detached from the body, and to which is still adherent the greater part of the sciatic nerve, which is carefully separated without injury from the surrounding tissues. When the nerve is brought into connection with a contracting muscle, an electric stimulus from the latter affects the nerve, and causes the muscle which it supplies to contract also (*Matteucci's induced contraction*). Sometimes also, if sufficient care be taken in the arrangements, by uniting with the nerve of the galvanoscopic foot the longitudinal and transverse sections of a muscle, a contraction of the galvanoscopic foot may be seen. This experiment, first somewhat roughly made by Von Humboldt, has been long known as *non-metallic contraction*, and has been regarded as a strong proof of the existence of animal electricity. (*Brücke.*)

b. *General Results.*—When a portion of the gastrocnemius muscle of a frog in a state of rest is placed upon the cushions of Du Bois-Reymond's apparatus above described, in such a manner that the transverse section touches the one cushion, and the longitudinal surface of the muscle the other, a deviation of the needle of the galvanometer indicates the existence of a current, which in the muscle passes from the transverse section to the surface of the muscle, and in the galvanometer circuit from the surface to the transverse section. The two surfaces manifest differences of electrical potential: the surface of the muscle is *positive*, while the transverse section is *negative.* If, in place of a transverse section of the muscle, we take the tendon of the muscle, which, as it contains the termination of the individual muscular fibres, may be regarded as the natural transverse section, it will be found also to be negative. On the other hand, if, in place of the natural surface of the muscle, we take a section of the muscle parallel to the muscular fibres, or, in other words, an artificial longitudinal surface, it will also be found positive. Thus it may be stated generally that *any natural or artificial longitudinal surface of a living muscle is positive to any natural or artificial transverse section.* Du Bois-Reymond has shown, and his experiments have been repeated by numerous observers, that the force and direction of the currents from different parts of the muscle are as follows:—(1) There is a strong deviation of the needle when the galvanometer circuit unites a longitudinal surface to a transverse surface, and the maximum of deviation is obtained when the middle of the longitudinal surface is connected with the middle of the transverse surface. (2) The deviation is small when the galvanometer circuit connects two points unequally distant from the middle of the surface, whether longitudinal or transverse, with two points unequally distant from the two opposite surfaces. (3) In longitudinal surfaces a point near the equator is always positive to any point nearer the ends of the muscle, and in transverse surfaces a point nearer the centre is always negative to a point nearer the surface of the section. (4) There is no deviation when the galvanometer circuit unites two points of the same surface, or two opposite surfaces equally distant from the centre, or the centres of two opposite surfaces. (5) Sometimes the tendinous part of the muscle, in place of being negative, may be positive to the surface of the muscle. This phenomenon is most frequently observed when the muscle is quite fresh, and has been submitted, whilst the animal was alive, to a low temperature for a considerable time; and this portion of the muscle has been termed the *parelectronomic* part. (6) If we make an oblique instead of a perfectly transverse section of a muscle, the most negative point of the section, instead of corresponding to the centre of the section, as is the case with a perfect transverse section, approaches the acute angle, and the most positive point of the longitudinal surface, on the contrary, approaches the obtuse angle: these are the facts regarding the electrical condition of what has been termed the *muscular rhomb.*

c. *Negative Variation of the Muscle Current.*—When the muscle is in a state of activity, a remarkable change occurs in its electrical condition. If the muscle be on the galvanometer cushions, in the manner already described, the deviation of the needle indicates the existence of the normal current. If then the nerve supplying the muscle be excited by a current from the induction coil, so as to throw the muscle into a state of powerful contraction, the needle swings back towards zero, thus indicating a diminution of the normal current, or the existence of a current in the opposite direction. This change in the state of the current has been termed the *negative variation.* It has been ascertained by most refined methods of investigation, conducted by Helmholtz, that the commencement of negative variation is about the $\frac{1}{200}$ of a second after the moment of the excitation of the muscle. But Von Bezold showed that in the nerve itself there elapses about the $\frac{1}{200}$ of a second between the instant when the excitant is applied to the nerve and when the nerve is excited. Consequently, the commencement of the negative variation of the muscle current coincides exactly with the moment of the excitation of the muscle. The negative variation, which first increases and then decreases, lasts about the $\frac{1}{300}$th of a second, and it is entirely gone before the muscle begins to contract, that is to say, it occurs during a portion of the period of latent stimulation (see p. 119). Bernstein has arrived at the conclusion that the negative variation travels with a rapidity of about 3 metres per second, which is the same rate as that of the wave of muscular contraction. Experiments by Meissner, Cohn, and Holmgren have thrown so much doubt upon some of these results of Bernstein as to render a repetition of the investigations desirable.

d. *Theories of the Muscle Currents.*—These may be briefly alluded to as four in number. (1) The *chemical* theory of Liebig: that the muscle current was due to the reaction of the alkaline blood upon the acid muscle substance. (2) The *electro-capillary* theory of Becquerel. He showed that electrochemical circuits may exist, as in the body, without the existence of a metal. Two liquids of a different nature, separated by a narrow slit or series of pores, or by an organic membrane, may give rise to a current; the wall which is in contact with the liquid next the acid acts as the negative pole, while the opposite wall is the positive—the walls of the capillary spaces acting as solid conductors. According to Becquerel, the tissues of the body present an infinite number of electro-capillary couples, which give origin incessantly to electric currents. Thus in the capillaries of the tissues, the face of the capillary wall in contact with the blood is the negative pole, whilst the face in contact with the fluid bathing the tissues is the positive pole. (3) *Physical* theory of Du Bois-Reymond. If we take a cylinder of zinc, having a bit of copper soldered on each side, and plunge it into water, there are formed an infinite number of isolated currents, which travel through the water from the zinc to the copper, and a part of which may be conveyed by conductors applied to the zinc and to the copper. If then a galvanometer be interposed in the circuit, it will be found that the zinc, forming the centre of the cylinder, is positive, and the copper, forming the sides, is negative, an arrangement similar to that of a muscle. Du Bois-Reymond has imagined therefore that each muscular fibre is composed of an infinite number of small electro-motor elements, analogous to the cylinder composed of zinc and copper above described. Each little element would have a positive equatorial zone, and two negative polar zones, and would be plunged into an intermediate conducting matter. The series of electro-motor elements in a muscle might be represented thus:

— + — — + — — + — — + — — + — — + —

or, supposing each element to be divided into two dipolar molecules, having the positive poles turned in the same direction, thus :

— + + — — + + — — + + — — + + — — + + —

(4) *Contact* theory of Hermann. Hermann denies the existence of muscular currents in a "perfectly uninjured, unskinned animal, the muscles of which are in a state of rest." While admitting the general accuracy of the observations above described, he supposes that the differences of electrical potential, which produce the currents, are due to injurious influences caused by the mode of preparation acting upon their surfaces. The fact that it appears to be impossible to prepare a piece of muscle, and to place it on the cushions of a galvanometer, without observing a current, in the manner already described, coupled with our knowledge of the existence of currents from the uninjured leaf of the *Dionæa muscipula*, or Venus' Fly Trap, which we owe to Burdon-Sanderson, leads us to be very cautious in abandoning the older views, and in accepting those of Hermann. It may be pointed out, also, that in no circumstances could we obtain evidence, by means of a galvanometer, of the existence of a current in a closed circuit or group of closed circuits, as is the case in living uninjured muscle, without so injuring the muscle as to break a circuit. The fact, therefore, that by a special mode of preparing the muscle, no current may be obtained, is no proof that no currents actually exist.

Muscle Current from Uninjured Man.—By placing each hand in a shallow vulcanite trough containing a weak solution of common salt, and connected by zinc terminals with a sensitive galvanometer, the existence of a current will be shown by a deflection of the needle. Suppose that the muscles of one of the arms are then thrown into a state of strong voluntary contraction, the needle of the galvanometer will swing backwards to zero, or perhaps to the other side of it, showing what might be regarded as a negative variation. It is very doubtful, however, if the phenomena so observed are due to muscle currents, and it is more than probable that they may be occasioned merely by changes in the amount of contact between the surface of the skin and the fluid.

Electro-tonic State of Muscle.—By this term is meant the condition of a muscle during the passage of a continuous current of electricity through it. It consists chiefly in a modification of the natural muscle current. When the constant current is in the same direction as the muscle current, in the interior of the muscle—that is, from the transverse section to the longitudinal surface—the muscle current is increased; when, on the other hand, the constant current is in the opposite direction to the muscle current, the latter is diminished.

6. PRODUCTION OF HEAT BY MUSCLE.

The apparatus required in investigating the thermal phenomena of muscle, consists of a galvanometer of small resistance, and a thermo-electric pile, or thermo-electric needles. All thermo-electric apparatuses are based on the fact of the development of electric currents on heating the junction in circuit of two dissimilar metals. The needles, which are more easily applied to a small muscle than a thermo-electric pile, are composed of two metallic wires, the one of iron and the other of copper, soldered together at one of their ends. One of these needles is kept at a constant temperature, while the other is passed through the muscle in such a manner that the junction of the metals is imbedded in the mass of muscle. The two ends composed of iron are united together by a wire of the same metal, and the two copper ends are put in connection with the galvanometer. By such an arrangement, it will be found that there is a deviation of the galvanometer needle when the muscle contracts, owing to the development of a thermo-electric current, from the metallic junction in the muscle being raised to a higher temperature than the other junction kept at a constant temperature in a vessel of boiling water, or in melting ice. Heidenhain has shown, by the use of extremely delicate arrangements of this nature, that the instantaneous excitation of the nerve supplying a muscle is attended by a rise of temperature in the muscle. The development of heat in a muscle depends—(1) upon its tension; (2) on the work done; and, (3) on the state of fatigue of the muscle. The more a muscle is stretched, the greater will be the amount of heat developed when it contracts. According to Beclard and Heidenhain, a muscle develops its maximum amount of heat, supposing the intensity of the stimulus to remain the same, when it is so stretched as to be unable to contract at all. The energy of a contracting muscle may be entirely transformed into heat; it may appear either as heat or mechanical work, or both. If we add the energy appearing in the form of heat in a contracting muscle to the energy developed as mechanical work, the sum is the total amount of energy expended during the contraction. The greater the heat, the smaller will be the mechanical work, and *vice versa*. It follows that the heat produced during work is, in the same time, inversely proportional to the amount of work. With regard to fatigue, it may be stated that as a muscle becomes exhausted by successive excitations, or by the approach of death, both the amount of work done and the production of heat simultaneously diminish. The two quantities, however, do not diminish equally: heat diminishes more rapidly than work, so that it is possible to have a muscle capable of performing a small quantity of mechanical work, but at the same time producing no heat. The venous blood, coming from a muscle in a state of activity, is warmer than that flowing from a muscle at rest; and it has been ascertained that the gastrocnemius of a frog, deprived of blood, will show an increase of about $\frac{1}{10}$th of a degree C. for each contraction, until it becomes much fatigued. Billroth and Fick determined in the muscles of mammalia, under the same conditions, a rise of 5° C. Leyden found a rise of temperature during tetanus in animals, and Wünderlich observed the same phenomena in patients suffering from tetanus; and, further, that the maximum temperature was not attained, in these cases, until after death.

7. GENERAL PHYSIOLOGICAL PROPERTIES OF MUSCLE.

1. *Nutrition.*—The nutrition of muscular tissue is very active. A muscle in a state of rest, and supplied with blood, absorbs oxygen and eliminates carbonic acid. During contraction, these changes are much increased, and the elimination of carbonic acid goes on more rapidly than the absorption of oxygen. It has also been ascertained that during contraction the substances that may be extracted by water from muscle are diminished, while those extracted by alcohol are increased. At the same time, the muscle becomes acid from the development of lactic acid, and the amount of acid formed increases with greater muscular activity. The circulation of the blood is more active in a contracting muscle than in one at rest. According to Bernard, at the moment of contraction the blood is retained in the capillaries, and does not enter the veins; it passes only into the veins in the interval of muscular contraction, and the blood flowing in the veins from a contracting muscle is dark and distinctly venous, whilst if the muscle is in a state of repose it is red and arterial. The exact nature of the

chemical processes happening in a muscle during contraction is still within the region of hypothesis and not of fact.

2. *Muscular Irritability.*—By this phrase is meant the property which living muscle possesses of responding to a stimulus, the visible indication of a response being a change of form, or a contraction. The term *contractility* is sometimes employed to denote the same fact. Irritability is a property inherent in the muscular fibre, a doctrine first clearly enunciated by Haller, and which, though frequently controverted, is upheld by all the experimental facts of the present day. The most convincing proof of the doctrine, first given by Bernard, is that if we poison an animal with curare, stimulation of the motor nerves produces no effect, while the direct excitation of the muscle is at once followed by contraction. It might be objected to this experiment that the persistence of irritability may depend on the integrity of the motor end-plates of the muscle, which may not have been affected by the poison; but, as was first shown by Kühne, if we examine with the microscope living muscular fibres from an animal under the influence of curare, it is possible to find fibres containing no motor end-plates, which are still capable of contracting on the application of a stimulus. The view of the inherent irritability of muscle is also supported by various other facts. Thus, sulphocyanide of potassium abolishes irritability without affecting the integrity of the nerve; electric currents of very short duration may excite the nerve without exciting the muscle; irritability may last several weeks after section of the motor nerves, whilst the excitability of the nerves is lost in about four days. Finally, irritability may be observed in structures having no nerves and consisting only of protoplasm, such as the contractile tissues of plants, the bodies of many of the Protozoa and Cœlenterata, the colourless blood corpuscles, spermatozoids, and cilia. When we remember that

the essential constituent of muscle is a form of protoplasm, one of the prominent phenomena of which is its capability of responding to a stimulus, it requires little evidence to convince us of the truth of Haller's doctrine.

Muscular irritability may be excited either by nervous action, its normal stimulus; or by *excitants*, which may be regarded as accidental, and which act directly on the muscle substance. Amongst the latter may be enumerated *mechanical* actions, such as tension, percussion, pricking, &c.; *physical* actions, such as the application of electricity and heat; *chemical* stimuli, such as ice-cold water, weak solutions of metallic salts, dilute acids, alkaline chlorides, ammonia, &c.

Muscular irritability may be increased or conserved for a considerable time by the following conditions:—(1) by an afflux of blood: if the lumbar nerves of a frog be divided on one side, the capillaries become dilated from paralysis of the vaso-motor nerves, and the irritability of the muscles is then much greater than on the uninjured side; section through one-half of the *medulla oblongata* and of the *corpora bigimena* is followed by hyperæmia, or increase of blood, and increase of irritability in one-half of the body; (2) Rest; (3) The presence of oxygen; muscles retaining their irritability longer in oxygen than in ordinary air, and still longer than in air deprived of its oxygen; the injection of oxygenated blood into a limb entirely separated from the body maintains irritability for a considerable time; (4) The action of certain substances, such as theine and veratrine; and (5) the passage through the muscle in a longitudinal direction of a very feeble continuous current of electricity.

Irritability is diminished or destroyed, by (1) arrest of the circulation; (2) fatigue; (3) a temperature considerably above or below the mean temperature of the muscle, which varies in different species of animals; (4) the presence in excessive quantity in the muscle of such substances as carbonic acid, lactic acid, phosphate of lime, and certain alkaloids. It is said that muscular irritability is almost instantaneously destroyed by large doses of sulpho-cyanide of potassium, all the salts of potash, the bile, emetine, upas antiar, &c.

After division of the nerves supplying it, and when the circulation is cut off, the irritability of a muscle disappears with great rapidity.

Irritability disappears more quickly after death from warm-blooded than from cold-blooded muscles. Thus, according to Brown-Séquard, irritability lasted in the muscles of the following animals :—

Rabbit,	8½	hours.
Sheep,	10½	,,
Dog,	11¾	,,
Cat,	12½	,,
Frog,	24 to 40	,,

In man it has been observed to last for even so long a period as 26 hours after death, but in most cases it disappears in the course of 5 or 6 hours. It vanishes quickly from the muscles of persons who have died from exhaustive diseases, but it may last a long time in well nourished muscles.

8. GENERAL PHENOMENA OF MUSCULAR CONTRACTION.

When a muscle, say the gastrocnemius, removed from the leg of a recently-killed frog, is caused to contract, it assumes the form of a globular mass which is about one-third of the primitive length of the muscle. In the living body, however, the shortening is never so great, as the two ends are stretched by the elastic force of the antagonist muscles and the resistance of the points of insertion. The amount of shortening of each muscle depends upon its length, and, for a given muscle, the shortening increases with the intensity of the stimulus and diminishes with the fatigue of the muscle.

When a muscle contracts, there is no change in its absolute volume. This may be demonstrated by placing the muscle in a small bottle filled with water, through the walls of which two fine platinum wires are fused for the purpose of conveying an electric stimulus to the muscle. The stopper of the bottle is drawn out into a long capillary tube, in which the fluid in the bottle ascends. It will then be found that, on causing the muscle to contract, the fluid in the capillary tube does not descend; that is to say, there is no diminution in volume.

Another mode of observing muscular contraction is to examine under the microscope, with a magnifying power of 300 diameters, a living muscular fibre removed from the leg of an insect. On stimulating the fibre at one end, an undulation will be observed to travel along the whole length of the fibre, and the transverse striæ approach each other. This phenomenon will be best observed when the muscle is slightly stretched. On adapting the polarizing apparatus to the microscope, it will be observed, as has been already stated, that the anisotropic portion is the seat of the contraction.

a. *Phases of a Single Contraction.*

The phenomena already mentioned may be noticed by the unaided eye or by the use of the microscope, but as they do not include all the phases of muscular contraction, many of which are of very short duration, recourse must now be had to various methods of accurate experiment. These are conducted with the aid of myographs, by which a graphic representation of the curve of muscular contraction may be obtained. The arrangement of the apparatus in this experiment is shown in Fig. 20.

The experiment is conducted as follows: The gastrocnemius muscle, the contraction of which is to be studied, is fixed by its tendon to the lever of the myograph (*c*), and the nerve is brought into contact with the electrodes; the recording cylinder (*a*) is then allowed to rotate, and when it has attained sufficient velocity, the key (*f*) in the primary circuit of the coil (*e*) is opened; a single induction shock is thus transmitted to the nerve, which causes the muscle to contract and to describe, by moving the lever of the myograph, the curve *a c d e*, in Fig. 21.

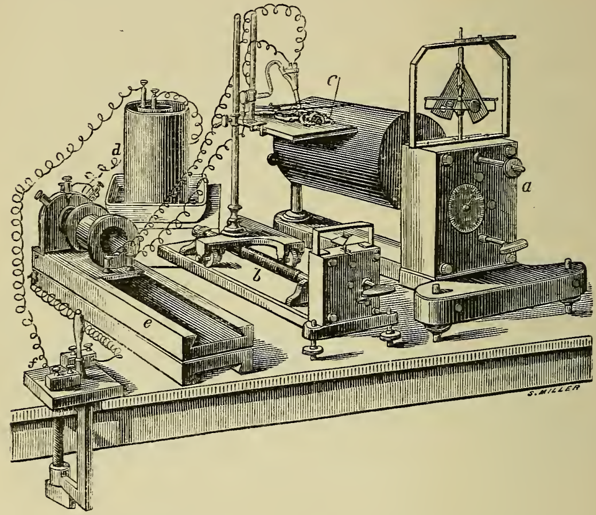


FIG. 20.—Arrangement of apparatus for obtaining the curve of a muscular contraction caused by a single induction shock; *a*, revolving cylinder; *b*, railroad carrying from left to right *c*, the myograph of Marey; *d*, galvanic element, connected with *e*, the primary coil of the induction machine; the wires from the secondary coil of the induction machine pass to the electrodes of the myograph, seen a little to the left of *c*; *f*, key interposed in the circuit of the primary coil.

On analysing this curve, it is seen to be composed of three unequal periods:—

(*a*) Suppose the muscle has received the shock at *b*, there is a short period represented by the line from *b* to *c*, in which no contraction occurs. This time, usually about the $\frac{1}{100}$th of a second, is called the *period of latent stimulation.* Its commencement and termination are easily registered by interposing in the primary circuit a signalling apparatus, which would draw on the cylinder the line *f g h i k;* while the time is recorded by a chronographic tracing *l m.*

(*b*) A second period, corresponding to the *contraction* of the muscle, indicated by the ascent of the curve *c d*, the duration of which is also registered by the chronograph, and which is sometimes rapid and sometimes slow.

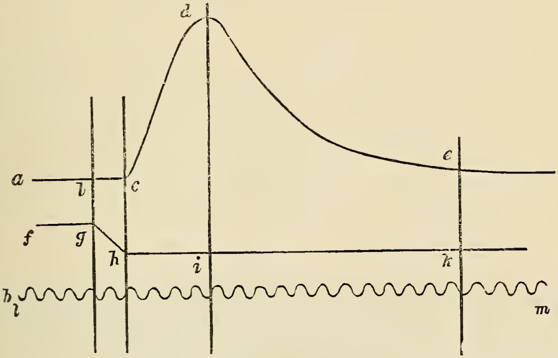


FIG. 21.—Curve of a muscular contraction, produced by a single induction shock. *a b c d e*, line drawn by the lever of the myograph; *f g h i k*, line drawn by electric signalling apparatus; *l m*, chronograph registering 100 vibrations per second.

(*c*) A third period of *relaxation*, represented by the descent of the curve *d e*, in which the muscle returns to its primitive length; this period is longer than the second, as indicated by the obliquity of the curve.

For purposes of comparison, it is often important to obtain a series of curves in juxtaposition. This may be done, with the arrangement above described, by sending the shock to the muscle a little later in each revolution of the cylinder, the myograph being stationary, when such a tracing as seen in Fig. 22 will be recorded.

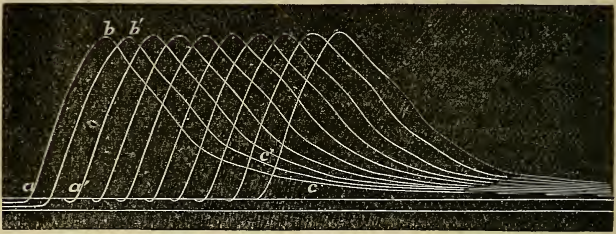


FIG. 22.—Tracings of muscular contractions produced by successive single induction shocks, to be read from left to right, thus—*a*, *b*, *c*.

Consecutive tracings may be still more elegantly obtained by placing the myograph on the railroad apparatus seen in Fig. 20 (*b*), which carries the myograph slowly along the surface of the cylinder. By causing the cylinder to interrupt automatically the primary circuit at the same moment in each revolution, the successive contractions will be registered as in Fig. 23.

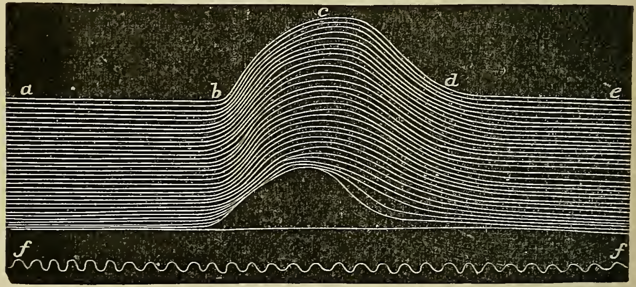


FIG. 23.—Contractions of the gastrocnemius muscle of a frog imbricated vertically. From below upwards the effects of fatigue may be observed in the gradual lengthening of the time of contraction. *ff*, the chronograph, registering 100 vibrations per second.

The *duration* of muscular contraction varies in different species of animals: very short in birds, somewhat less in mammals and fishes, and prolonged in reptiles. The amplitude of the curve, indicating the *amount* of muscular contraction, increases with increase of the stimulus, at first rapidly, then more and more slowly, and when a maximum is reached, it remains constant, as indicated by the amplitude of the curve remaining the same. Fatigue diminishes the amplitude and increases the duration of the contraction, as seen in Fig. 23. Stoppage of the circulation and cold has the same, whilst the gentle application of heat has the reverse, effect.

When a living muscle is stimulated, it not only contracts, but becomes thicker. The movement of *thickening* has been traced graphically by Marey, and the curve has been found to be generally the same as that of contraction.

As has been already mentioned, if a stimulus be applied to one end of a living muscular fibre, a kind of wave is seen to propagate itself towards the other end. This has been termed the *wave of contraction*, and its rapidity has been measured by Marey with the aid of delicate appliances, which, as they are applicable to the registration of other physiological phenomena, may be here shortly described.

b. *Marey's Mode of Transmitting Movement.*

One of the chief obstacles in the registration of animal movements is the difficulty of attaching directly to the body a marker which will inscribe on a blackened surface the phases of the movement. It is therefore necessary to have means of transmitting the movement to a distance, or, in other words, transferring to the recording surface the movement we wish to examine. This Marey has accomplished by the use of *tambours*, or drums, united by tubes containing air. One of these tambours is seen in Fig. 24.

It consists of a shallow metallic case, or drum, the upper surface of which is formed by a thin indiarubber membrane supporting the writing lever. Two tambours, each having a short metallic tube communicating with their interior, may be connected together by carrying an indiarubber tube from the one metallic tube to the other, as represented in Fig. 25.

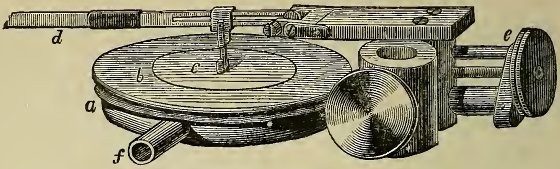


FIG. 24.—Tambour of Marey. *a*, metallic case; *b*, thin indiarubber membrane; *c*, thin disc of aluminium supporting the lever *d*, a small portion of which only is represented; *e*, screw for placing the support of the lever vertically over *c*; *f*, metallic tube communicating with the cavity of the tambour for attachment to an india-rubber tube.

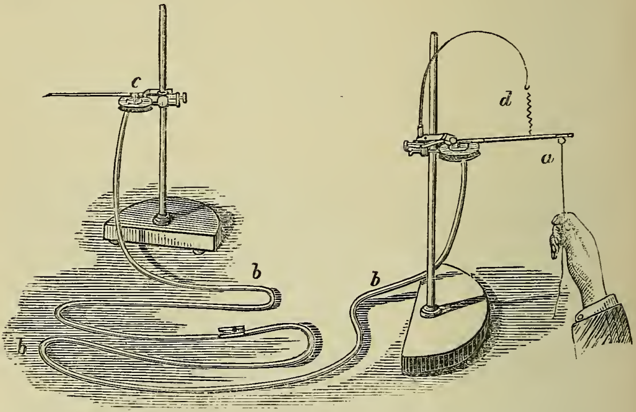


FIG. 25.—Tambours of Marey arranged for the transmission of movement,—*a*, receiving tambour; *b*, india-rubber tube; *c*, registering tambour; *d*, spiral of wire, by the elasticity of which, when the tension is removed from *a*, the lever ascends.

On depressing the membrane of the first tambour, part of the air which it contains is expelled; this air passes through the indiarubber tube into the second tambour, the membrane of which, carrying the lever, is elevated. On the contrary, when the first tambour is not acted upon, the membrane of the second returns to its former position. The first may be termed the *receiving*, and the second the *registering*, tambour. It will be observed that, as above arranged, the movements of the registering tambour are the reverse of each other: when the membrane of the one is drawn downwards, that of the other is forced upward. When it is

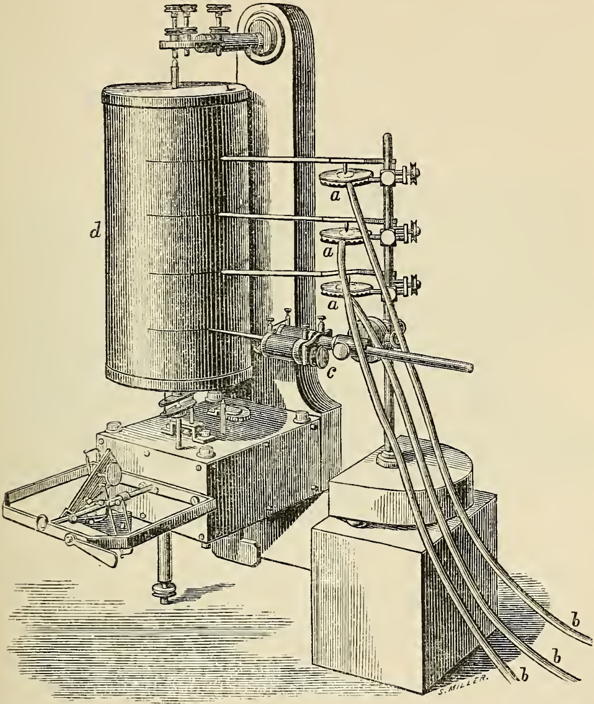


FIG. 26.—Arrangement of registering tambours, *a a a*, for recording three movements on cylinder *d*. The tubes communicating between the recording and registering tambours are seen at *b b b*. Chronograph, *c*.

desirable to obtain the movements of the levers in the same direction, one of the tambours must be reversed. The most beautiful application of this method of transmission of movement is that it is possible to register upon the same recording surface a series of movements occurring in different localities, so as to have the means of comparing their rhythm, duration, and character. In Fig. 26, an arrangement is represented by which three movements, along with a chronographic tracing, may be obtained on the same cylinder.

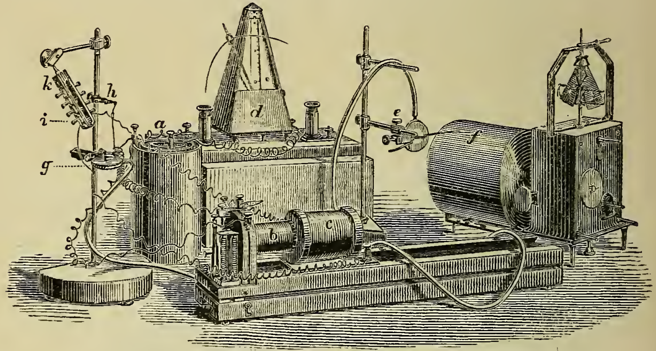


FIG. 27.—Arrangement of apparatus for transmission of muscular movement by tambours: *a*, galvanic element; *b*, primary coil; *c*, secondary coil of induction coil; *d*, metronome for interrupting primary circuit, when induction current is sent to electrodes *k*; *h*, forceps for femur; the muscle, which is not here represented, is attached to the receiving tambour *g*, by which movement is transmitted to the recording tambour *e*, which writes on the cylinder *f*.

Marey has also applied his method of transmission of movement to the phenomena of muscular contraction. By causing the contracting muscle to act on a tambour, as seen in Fig. 27, the movement may be carried to a distance to a recording tambour in connection with a cylinder. By this ingenious method it is possible to subject the muscle to different temperatures, or to the action of various gases, without interfering in any way with the recording apparatus.

c. *Wave of Muscular Contraction.*

Marey has measured the rapidity of the wave which passes along a contracting muscle by placing upon it two small receiving tambours, at a certain distance from each other, and each connected with a registering tambour. On stimulating one of the ends of the muscle, the thickening which accompanies its contraction, as it passes from one end to the other, acts upon the two receiving tambours successively, and a tracing is obtained such as is seen in Fig 28.

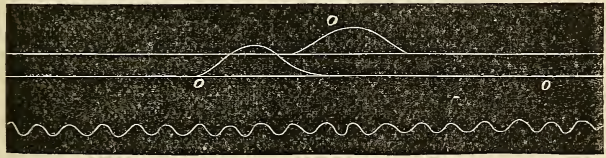


Fig. 28. Tracing of the propagation of the muscular wave. Chronographic tracing, 100 vibrations per second underneath. (*Marey.*)

It will be seen that the two curves do not coincide, and the distance between their summits gives the rapidity of propagation of the muscular wave, which is from one to three metres per second. The wave of contraction excited in a muscular fibre is limited to it alone, and is not transmitted to neighbouring fibres.

d. *Contraction produced by a Series of Rapid Shocks.*

A rapid series of induction shocks may be sent to a muscle by means of Du Bois-Reymond's electro-motor, seen in Fig. 16. The shocks sent by the apparatus, when the primary circuit is automatically closed and opened, may be regarded as instantaneous excitations. When excitations, by induction shocks, exceed a small number, say three or four per second, the muscle contracts more strongly, and the contraction continues for a longer time, than if the muscle had received a single shock of the same intensity. This observation may be readily made by interrupting the current of the induction coil by means of a metronome, so that the number of shocks sent per second may be varied at pleasure. In these experiments it is also advantageous to take the tracings on a smoked glass plate, according to the method of Fick. It will then be found that the opening shock is more powerful, as shown by the amount of muscular contraction, than the closing shock. When the shocks succeed each other regularly, at the rate of about fifteen per second, and in such a way that the duration of the interruption is short compared with the duration of the shock, the muscle remains persistently contracted. This state of permanent contraction is called *tetanus*, and its phases must be more carefully studied.

Tetanus.—When a muscle is stimulated by an induction machine, it draws a curve on a moving surface which is different in character from that of a single shock (see Fig. 21, p. 119). Such a curve is shown in Fig. 29.

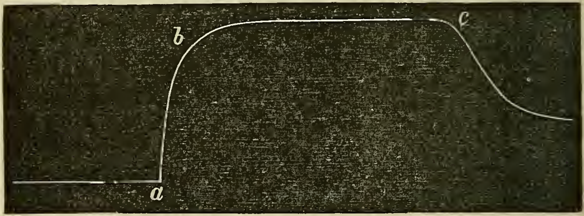


FIG. 29.—Tetanus produced by numerous shocks from an induction machine. The interrupted current acted at *a*, the lever rises rapidly, and at *b* the muscle reaches the maximum of contraction. The contraction lasts until *c*, when the current is shut off and the muscle slowly relaxes.

It is important to note that when a muscle is tetanized by an induction current, it contracts suddenly, as indicated by the rapid rise of the lever, that tetanus is a condition which lasts for a considerable time, and that the muscle relaxes slowly. Contrast Fig. 21 with Fig. 29.

When a series of induction shocks are more slowly transmitted to the muscle in contact with Marey's myograph, by interrupting the primary current by a metronome, the following tracing is obtained (Fig. 30):—

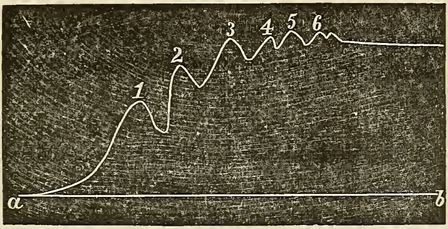


Fig. 30.—Tracing of a muscle passing into a tetanic state; when the primary current of an induction machine is rapidly made and broken by a metronome. The first shock was transmitted to the nerve at *a*, the second an instant after 1, the third an instant after 2, and so on. It will be observed that with each succeeding shock the muscle becomes shorter, though the shortening at each shock is less.

A number of distinct oscillations will be observed in the ascent of the curve. Each oscillation is somewhat shorter than the one immediately preceding it. Three cases in which a muscle is excited by successive shocks present themselves for consideration:—

1. When a second excitation acts after the termination of the contraction occasioned by the first, it produces a second muscular contraction having the characters of the first, and so on, as regards successive excitations, until the muscle becomes fatigued.

2. If the second excitation act during the period of latent stimulation following the first, the shortening is not greater than for one excitation, and the curve of contraction is the same.

3. If the second excitation act during the two last periods of the preceding contraction, the shortening corresponding to the second excitation is added to that of the

first. The curve thus produced is seen in Fig. 31. If other excitations quickly follow, each capable of causing a partial contraction, a state of permanent contraction or tetanus is produced, which is the sum of the partial contractions resulting from the successive shocks. Tetanus may be maintained for a considerable time, which varies according to the degree of vitality of the muscle, but by degrees it passes off, and the muscle slowly returns to its original length, under the influence of fatigue. When shocks are transmitted with too great rapidity, so as to be too short in duration, tetanus is not produced.

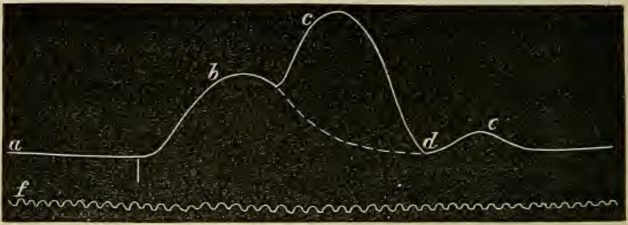


FIG. 31.—Tracing of a double muscle curve. While the muscle was engaged in the first contraction (whose complete course, had nothing intervened, is indicated by the dotted line), a second induction shock was sent to it, at such a time that the second contraction began just as the first was beginning to decline. *a*, *b*, first contraction; *c*, *d*, second contraction; *f*, chronographic tracing. (*Foster.*)

e. *Other Modes of Exciting Muscular Contraction.*

In addition to the normal stimulus transmitted by a nerve, and to the stimulus of electricity, muscular contraction may be excited by mechanical, thermal, and chemical stimuli.

1. *Mechanical Stimulus.*—The action produced by a mechanical stimulus depends upon the intensity of the stimulus and the rapidity with which it acts. Pressure upon a muscle, if slowly applied, may not excite a contraction, but if the pressure be made suddenly, contraction may be the result. When a muscle is stimulated by any

mechanical excitant, the result is not only a contraction passing from the excited point through the whole of the muscle, but a permanent contraction of the point touched. This contraction, termed by Schiff, its discoverer, *idio-muscular contraction*, may be observed in the living man when a blow is struck with a blunt body across a muscle, and perpendicularly to the direction of its fibres. There is then a contraction which extends the whole length of the muscle,

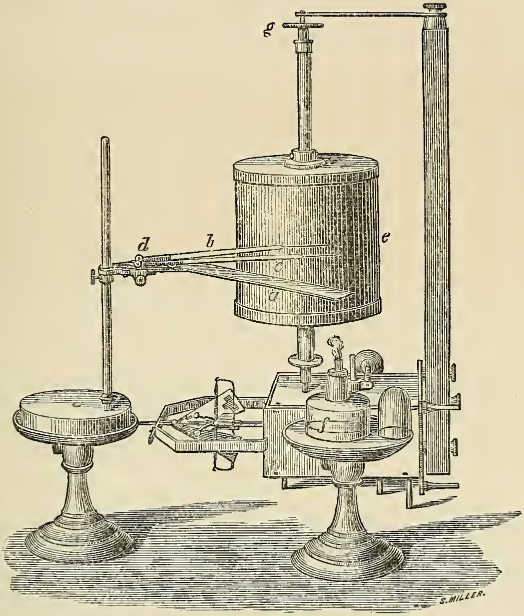


FIG. 32.—Arrangement for studying the action of heat on a frog's heart. A copper plate, carrying at one end two delicate levers, *b*, moving on a joint at *d*; the heart is placed underneath the levers near *d*, one on the auricular and the other on the ventricular portion, and the movements of the levers are recorded on the cylinder *e*, which may be gradually elevated, so as to obtain a continuous tracing, by turning the screw *g*. When heat is applied by the spirit lamp *f*, to the end of the copper plate, the heart beats faster and faster until it passes into a state of tetanus, from which it may recover by cooling the copper plate with a piece of ice.

and when this contraction has disappeared, there remains at the point of excitation a transverse swelling, which lasts for a certain time. A muscle may pass into a state of tetanus, on irritating, by successive mechanical shocks, the nerve supplying it. This may be accomplished by the mechanical tetanomotor of Heidenhain, which consists of a small hammer, kept in movement by an electro-magnet, through which a current passes at rapid and regular intervals. The hammer is made of ivory, and strikes upon the nerve lying in an ivory groove.

2. *Thermal Stimulus.*—The passage of a muscle from one temperature to another may excite muscular contractions, and when the temperature is raised to about 60° C., tetanus is produced. This fact is strikingly illustrated by the action of heat on the heart of a frog, an experiment which may be readily performed by the arrangement shown in Fig. 32.

3. *Chemical Stimulus.*—A great number of chemical agents produce contractions by their influence on the chemical composition of the muscle or of the nerve supplying it. Amongst the agents which excite contraction are the fixed alkalies, the mineral acids, acetic, oxalic, tartaric, and lactic acids, alcohol, ether, kreosote, the neutral alkaline salts, such as chloride of sodium, and sulphates and carbonates of the alkalies, very concentrated solutions of metallic salts, and concentrated solutions of urea, sugar, and glycerine. All of these substances probably excite either the nerve or the muscle by absorbing water, and the kind of contractions obtained resemble those following rapid drying of a nerve by exposure to the air. Distilled water injected into the bloodvessels of a muscle excites contraction, but it rarely excites contraction when applied directly to the nerve or muscle.

f. *Muscular Work.*

The amount of work done by a healthy muscle in lifting a weight will vary according to the strength of the stimulus and the weight to be lifted. A few experiments made by Fick's method, in which the muscle is stimulated by single induction shocks of equal intensity, will show this clearly.

a. The Contraction as a Function of the Stimulus.—Suppose the gastrocnemius muscle of a frog is loaded with say a weight of 10 grammes, and the apparatus is arranged for a single induction shock. Removing the secondary coil of the induction machine to a considerable distance from the primary, let a single shock be sent to the muscle. If no contraction follow, let the secondary coil be removed nearer the primary until the first visible contraction is obtained and recorded. Then advancing the secondary coil onwards a definite distance nearer the primary each time, let each contraction be recorded as an ordinate on the abscissa line at distances proportionate to the distances the secondary coil is moved. A diagram may thus be constructed such as is seen in Fig. 33.

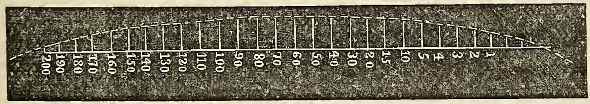


Fig. 33.—Diagram of muscular contractions, with the same weight and an increasing stimulus. The numbers represent the distance of the secondary from the primary coil, reading from left to right.

This diagram shows that the amount of contraction increases with the increase of stimulus, at first rapidly, then more slowly, until a maximum is reached; the maximum remains for some time, and afterwards the amount of contraction becomes less owing to the fatigue of the muscle from repeated stimulations.

β. The Contraction as a Function of the Resistance.—Suppose in this experiment the intensity of the stimulus is the same, while the load which the muscle has to lift is gradually increased. Let a contraction be recorded when there is no load to the muscle at all. Then load successively with 10, 20, 30, &c., grammes, recording the several contractions at proportionate distances along the abscissa line, as seen in Fig. 34.

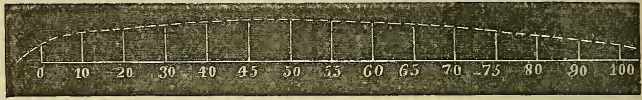


FIG. 34.—Diagram of muscular contractions with the same stimulus and increasing weights. The numbers represent grammes.

This diagram shows that as the weight is increased from zero upwards, the contraction increases; as the weight continues to be increased, contraction also increases, but more slowly, and beyond a certain point increase in the weight is followed by a diminution in the amount of contraction.

γ. Measurement of the Work done.—This is accomplished by measuring the actual amount of shortening of the muscle by the weight lifted. Let W be the weight and H be the height to which W is lifted, then $W H = x$, the work done. Suppose, for example, a muscle lifts 10 grammes 20 millimetres in height, the work done is 200 gramme-millimetres. This may also be shown diagrammatically by drawing an abscissa line, marking off upon it the distances proportionate to different weights, and drawing as ordinates the actual work done in the case of each weight. A line drawn through the summits of the ordinates will give the curve of the work done with the same stimulus and increasing loads. (*Foster.*)

Weber has given the following figures with reference to the work done by the muscle of a frog:—

Weight Lifted in Grammes.	Height in Millimetres.	Work done in Gramme-Millimetres.
5	27·6	138
15	25·1	376
25	11·45	286
35	6·3	220

This table shows that the work increases with the weight until a certain maximum, after which a diminution occurs more or less rapid according as the muscle is fatigued.

Static Force of a Muscle.—In charging a contracting muscle with gradually increasing weights, there arrives a time when the elongation due to elasticity exactly compensates the contraction of the muscle. When this is so the muscle is, as it were, in a state of equilibrium, and the weight expresses what Weber termed the static force of the muscle. This force he found in the frog's muscle to be 692 grammes for a transverse section of a square centimetre, and Henke and Koster have estimated the static force of the muscles of the calf of a man's leg to be from 8 to 9 kilogrammes.

g. *Muscular Fatigue.*

A muscle becomes fatigued after increased work. Up to a certain point the substances produced in a contracting muscle are eliminated as quickly as they are formed, and at the same time new materials necessary for the repair of the muscle are supplied. There is thus, as it were, a balance between the two processes. When, however, the muscle is excited to very frequent contraction, the products of waste accumulate in the muscle, and probably also sufficient time is not allowed for the supply of reparative material. Fatigue diminishes the cohesion of muscle, it has apparently little or no effect upon its elasticity, it lowers irritability, and it lengthens the period of latent stimulation. The contraction of a fatigued muscle is of smaller amplitude and of longer duration, as seen in Fig. 23, p. 120. During fatigue a muscle returns to its original length more slowly after a contraction. As has been already stated, the work done diminishes rapidly during fatigue.

According to Kronecker, a muscle is fatigued more quickly when it works than when it contracts without accomplishing work, or when it is in tetanus. The fatigue which follows work depends upon the amount of the resistance to be overcome by the work, and the time during which the resistance acts against the muscle. The capacity for work diminishes with the elevation of temperature, and if the temperature do not pass a certain limit, about 40° C. for the muscle of a frog, the muscle may recover its original power by the application of cold.

h. *The Muscular Sound.*

When a stethoscope is firmly applied over a powerfully-contracting muscle, such as the biceps in a muscular man, a deep tone is heard, which is produced by about twenty vibrations per second. It may also be heard during profound stillness, as in the middle of the night, on stopping the ears and powerfully contracting the muscles of mastication. The muscular sound, according to Helmholtz, is produced by the successive shortenings which, as we have seen, make up a muscular contraction.

It is probable that the sound heard is not that due to twenty vibrations per second, which number of impulses on the ear would not produce the sensation of a tone, but to forty vibrations per second, or the first harmonic of the prime tone.

The existence of the muscular tone renders it probable that to secure the contraction of a voluntary muscle in man during life, from twenty to thirty impulses per second are transmitted from the nerve-centres to the muscle along the motor nerves.

i. *Cadaveric Rigidity.*

Soon after death, muscles become firm and solid; they oppose a great resistance to extension, and when extended do not return to their original length. Their tonicity has disappeared, so that when cut across they do not retract. The muscle substance, when seen in thin section, has lost its transparency. In this condition, also, muscular irritability has been lost, but within a certain limit of time after its disappearance it may return on injecting arterial blood into the arteries. The muscle is strongly acid, a reaction due to the presence of lactic and carbonic acids. Cadaveric rigidity is due to coagulation of myosine. Rigidity may commence from a quarter of an hour to twenty hours after death. It occurs more quickly in exhausted than in well-nourished muscles. It lasts from several hours to several days, and when it comes on slowly, as in the muscles of a healthy well-nourished man killed accidentally, it lasts for a long time. After cadaveric rigidity has passed off, putrefaction begins.

Various theories have been advanced as to the intimate nature of muscular contraction, but they are too vague and of too little practical import to fall within the design of this work.

B.—NON-STRIATED MUSCULAR FIBRE.

1. STRUCTURE OF NON-STRIATED MUSCLE.

This variety of tissue consists of a large number of fusiform nucleated cells, forming a series of flattened bands. The colour of involuntary as contrasted with voluntary muscles is generally pale; the fasciculated arrangement of their fibres less distinct; the fasciculi smaller, and presenting frequent interlacement or reticulation with each other, by the union of whole bundles or of portions of them; there is a less quantity of connective tissue separating the fasciculi from each other; and there is generally a total absence of tendinous attachment of the fibres. The fasciculi of involuntary muscular fibres are also, for the most part, disposed in layers round hollow or tubular cavities, the fibres in some instances running in a longitudinal direction corresponding to the axis of the tube, but more frequently in a transverse or circular manner. The single muscular fibres of the involuntary muscles are of a much smaller size than those of the voluntary muscles, their diameter being generally from $\frac{1}{2000}$ to $\frac{1}{3000}$ of an inch. They have the form of somewhat flattened and prismatic fibres, in which it is impossible to perceive a tube of sarcolemma and distinct sarcous elements. The fibres are destitute of any regular transverse striæ, but in favourable circumstances for observation they present an obscurely granular appearance, which indicates that the substance of involuntary muscular fibre may be composed of imperfectly formed sarcous elements. The observation of minute single contractile fibrillæ in some of the lower animals, even though distinct striæ are absent, supports this view.

The bloodvessels have nearly the same mode of distribution as in the voluntary muscles. The nerves are principally derived from those of the ganglionic system. The muscular substance of the heart agrees with the other involuntary muscles in its general arrangement; but its colour and minute structure resemble, in some respects, more nearly those of the voluntary muscles. The fibres are intermediate in size between those of the two kinds, and present in general very obvious striæ, and frequently a tendency to division and apparent anastomosis.

2. Physical and Chemical Properties of Non-striated Muscle.

The physical properties of non-striated muscular tissue, such as cohesion, elasticity, &c., have not been investigated with sufficient precision to warrant distinct statements about them. The chemical constitution of the tissue does not appear to differ from that of striated muscular fibre.

3. Vital Properties of Non-striated Muscle.

When stimulated, either directly, by mechanical, chemical, or thermal stimuli, or by a nervous impulse, involuntary muscle contracts. The period of latent stimulation is longer than in striated muscle, and the contraction takes place slowly, and lasts for a lengthened period. The general character of the contraction may be seen in the movements of the intestine of a recently killed warm-blooded animal. Paul Bert has succeeded in obtaining a tracing of the

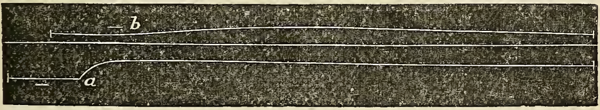


Fig. 35.—Tracing of the contraction of non-striated muscular fibre. The upper line was obtained from the contracting stomach, and the lower from the contracting bladder of a dog. The horizontal mark indicates the moment of application of the stimulus. In this tracing, 1 centimetre = 6 seconds.

contraction of non-striated muscle, as manifested by the movement of the walls of a viscus, which is shown in Fig. 35.

Marey has shown that the contraction of non-striated muscle is not made up of a series of lesser contractions, as in striated muscle, but of one single contraction, which may be of greater or less duration. According to Englemann, a stimulus applied to a group of non-striated fibres is propagated to neighbouring fibres, and thus the stimulus may radiate in various directions, even in tissues containing no nerves. The interesting observations of Foster on the contractions of the heart of a snail, and of Romanes on the transmission of impulses in the bodies of *Medusæ,* support the statement. Organs containing non-striated muscle frequently show rhythmical movements.

It is difficult to estimate experimentally the work done by this kind of fibre, but when we consider the force of the bladder in expelling urine, and still more the force of the uterus in parturition, it must evidently be very great. Nothing definite is known regarding the conditions of fatigue. According to Beaunis, the state of cadaveric rigidity occurs to a slight extent.

In ordinary circumstances, organs composed of non-striated muscle are only feebly sensitive, but occasionally they become so sensitive as to give rise to ill-defined sensations of discomfort, or even of pain.

Distribution of Muscular Fibres.—Striated fibres exist in all the voluntary muscles of the body, and in a few muscular parts not directly under the control of the will, as in the heart, pharynx, and upper part of the gullet, tensor tympani, and muscles covering the urethra, &c. Unstriated fibre is found in the lower part of the gullet, and thence throughout the whole alimentary canal (except the sphincter), in the urinary bladder, ureters, and urethra, in the uterus, vagina, and Fallopian tubes, in the trachea and bronchial tubes, and in the iris.

The following is an enumeration of some other parts exhibiting the phenomena of contractility, but without the obvious muscular character of most of the preceding. In these parts contractility is due to muscular fibres, analogous to those of the unstriated kind. 1. Circular fibrous coat of the arteries and absorbent vessels. 2. Excretory ducts of most of the glands, wall of the gall-bladder, &c. 3. Tunica dartos, skin of the nipple, and in the true skin generally. In all of these situations, fibres having the same characters as those of the involuntary muscles, exist either in considerable quantity separately, or mixed in smaller proportion with the other structural elements of the part, and where connective tissue abounds, it is frequently by no means easy to identify the few involuntary fusiform cells that may be present. (*Allen Thomson.*)

Consult PROCHASKA, De Carne Musculari in Oper. Min., 1800; BOWMAN in Trans. Roy. Soc. London, 1840, and art. Muscle in Cyclop. of Anat. and Physiol.; TODD and BOWMAN, Anat. and Phys.; and SHARPEY and SCHÄFER in Quain's Anat., eighth ed., vol. II, pp. 107-125; MAREY, Du Mouvement dans les Fonctions de la Vie, 1868; WUNDT'S Physiologie Humaine, p. 372 *et seq.*; BEAUNIS' Physiologie, p. 259, *et seq.*; for full details as to the experimental study of the functions of muscle, see account by MICHAEL FOSTER in Handbook for the Physiological Laboratory, p. 341; also CYON'S Methodik der Physiologischen Experimenti und Vivisectionen, Fünftes Capitel. For sketches of apparatus, see the Atlas of the same work, and also GSCHEIDLEN'S Physiologischen Methodik. FOSTER'S Text Book of Physiology, p. 33, *et seq.*; also MAREY'S Animal Mechanism, chaps. IV, V, and VI. As to the production of heat in muscular work, see MATTEUCCI, Sur les Phénomènes Physiques et Chemiques de la Contraction Musculaire (Comptes Rend., 1856, t. XLII); J. BÉCLARD, De la Contraction Musculaire dans ses rapports avec la Témperature Animale (Arch. Génér. de Méd., 1861, 5e série, t. XVII, p. 24); HEIDENHAIN, Mechanische Leistung, Warmentwicklung und Stoffumsatz bei der Muskelthätigkeit, Leipzig, 1864; Wundt, Physique Médicale, p. 535. For full details in matters relating to electro-physiology, see Morgan's Electro-Physiology; Du Bois-Reymond's Untersuchungen uber thierische Electricität, t. I et II. A *résumé* of all that was previously written on this subject is given in Du Bois-Reymond's work. Consult also Bland Radcliffe on Muscular Motion, Lond., 1876.

V.—CARTILAGINOUS AND OSSEOUS TISSUES.

Without entering into minute histological details, for which reference is made to works on histology, it is necessary to state briefly the facts regarding cartilage and bone.

1. General Structure of Cartilaginous Tissues.

These very firm and elastic substances are employed in the skeleton, and in some other parts of the body, when strong union, with some degree of yielding, or where great smoothness, and consequent free motion of the articular surfaces of bones on one another are required, and they are also made use of when a particular form is to be maintained in soft, moving parts, without adding greatly to their weight, and where the shock of sudden concussions is to be prevented by elasticity. Cartilage also forms a temporary frame-work for the soft parts during fœtal life, and by degrees gives place to the firmer frame-work of the osseous skeleton, characteristic of adult life.

Two kinds of these textures are to be distinguished—viz., *Cartilage and Fibro-cartilage*, the latter passing in some instances into an entirely fibrous substance.

Cartilage Cells.—These are round, oval, or crescentic in form. They consist of a mass of homogeneous or slightly granulated protoplasm, which contracts on the application of an electrical stimulus. Lying amongst the protoplasm there is always a small nucleus, and frequently there are also minute globules of oil, or particles of finely molecular mineral matter. Cartilage cells multiply by endogenous cell formation.

There are several varieties of each of the cartilaginous textures, which differ in their anatomical structure, physical properties, and chemical composition.

1. *True Cartilage* consists of a firm, clear matrix, in which are embedded numerous minute cells. To this form belong (1) *temporary* cartilage, which precedes ossification in the different bones; and (2) *permanent* cartilage, among which may be enumerated articular or hyaline, nasal, laryngeal and tracheal, costal and xiphoid cartilages.

2. *Fibro-cartilage* consists of two varieties. (1) The soft, spongy, or yellow fibro-cartilages consist of cells which are embedded in a felt-like fibrous matrix. The cartilages of the external auricle and meatus, the Eustachian tube, the epiglottis, and the small bodies of Santorini and the tarsal plates belong to this division. (2) White fibro-cartilage consists of a mixture of cartilaginous cells with a fibrous texture, and in many of the parts formed of this substance the quantity of fibrous texture greatly preponderates over that of the cells, and in some, indeed, entirely excludes them. To the various kinds of this texture belong the intervertebral substance, the uniting substance of the pubic and sacro-iliac symphyses, the interarticular plates of the sterno-clavicular, temporo-maxillary, knee and wrist-joints; the substance serving to deepen the borders of the acetabulum and glenoid cavity of the shoulder-joint; the tendinous sheaths, and the sesamoid bodies occurring in some of the tendons; but some of these, which are rather fibrous than cartilaginous plates, are covered with a thin layer of true cartilage. (*Allen Thomson.*)

There are some kinds of true cartilage which make an approach to the spongy form, such as the costal cartilages; in these the solid matrix is not so clear, but presents a granular, and even, in some instances, a slightly fibrous structure. This fibrous appearance of the matrix is not perceptible in youth, and increases as life advances.

In articular cartilage the cells are arranged in groups, which, towards the surface, are disposed in laminar plates lying parallel to the surface of friction; but in the other parts of it they generally present rather the appearance of short columns placed perpendicularly to the surface.

In true permanent cartilage the solid matrix has generally, in the mature state, encroached upon the wall and cavity of the cells, so as to cause their partial obliteration. In the young state of true cartilage, and in the spongy cartilages, the separate cells are much more easily perceived.

All the cartilages (excepting the articular) and the fibro-cartilages are covered by a fibrous membrane, the *perichondrium*, in which the bloodvessels ramify in considerable quantity. These bloodvessels penetrate into the fibrous parts of some of the fibro-cartilages, but rarely into the true cartilages. In some, as the costal cartilages, though not distributed minutely in the texture, the bloodvessels pass into cavities within it; and this is observed also in the cartilage of ossification, near the ossifying surface.

Cartilage is originally developed from a cellular blastema. In the first stage the cells are set close together in a fluid or soft substance which is in small quantity. Subsequently an intervening solid substance makes its appearance between the cells, and by its increase and encroachment upon the cavities of the cells, it separates them to a greater distance from each other. The farther growth of cartilage is believed to take place, in part by the endogenous production of cells within those previously existing, and in part by the independent formation of new cells, or their development from nuclei, in the solid blastema or intervening substance; the matrix, at the same time, probably also extending itself in some degree.

2. General Structure of Bone.

The substance of bone, which composes the hardest part of the skeleton, is best known in the dried state, when it has been freed by previous maceration from some other matters, which, in the recent state, are combined with it, 1st, A fresh bone consists of the *osseous substance* arranged in a more or less compact or loose form in various parts of the bones; 2nd, The cavities of the harder bony substance are filled with the fatty *medulla* or *marrow*, and with the areolar tissue and cells, and are permeated by bloodvessels, &c.; 3rd, The external surface of the bones (excepting at the articular surfaces, which are tipped with cartilage) is covered by a dense fibro-vascular membrane, the *periosteum;* and the larger cavities within the bones are lined by a more delicate membrane, termed medullary membrane or *endosteum.* Small bloodvessels run into the substance of bone from the periosteum through numerous pores over all the outer surface; and, in a variety of situations, more especially towards the extremities and borders of the bones, larger bloodvessels pass into the interior through foramina of a considerable size.

Pores may be detected even in the most compact substance of bones; these pores, which may be seen in a broken portion of the compact substance of bone, are the ends of a set of tubular reticulated passages, called *canals of Havers,* which run everywhere through the bone, some of them opening on the exterior, others in the medullary cavity or in the cancelli of the bone. The diameter of these passages varies from $\frac{1}{200}$ to $\frac{1}{1000}$ of an inch; they transmit blood-vessels through the compact bony substance.

In viewing thin polished sections of the compact bony substance with the microscope, it is seen to be arranged in *laminæ*, the greater number of which are concentrically arranged round the Haversian canals, while others are parallel to the walls of the cancelli, or to the inner and outer surface of the whole bone. Between these laminæ are observed dark, elongated, lenticular, jagged spots, which are termed *lacunæ*, being in dry preparations cavities in the hard bony substance. In living bone, each lacuna is occupied by a small, irregularly shaped mass of protoplasm, called a *bone-cell.* Sometimes the bone-cell has a stellate form, and the radiating processes pass into the canaliculi about to be described. Farther, the bony laminæ are observed to be traversed by fine tubes, which appear to radiate from the lacunæ in a somewhat irregular manner, and form fine and very numerous passages between the different lacunæ, and from them through the bony laminæ, on the one hand, to the external surface of the bone, and on the other, to the internal surface of the Haversian canals, cancelli, or medullary cavity. These fine tubes or *canaliculi* transmit fluids. They are from $\frac{1}{12000}$ to $\frac{1}{25000}$ of an inch in diameter, the lacunæ being from $\frac{1}{1000}$ to $\frac{1}{2000}$.

The nature of the smallest or ultimate particles of the solid bony substance lying between these canaliculi has not yet been exactly ascertained. The concentric arrangement of laminæ in bone, may still be clearly perceived in the animal part, from which the earthy matter has been removed by an acid; and, further, it is found that each lamina may be torn into much finer layers or thin shreds, which appear to consist of very minute crossing or interlaced fibres, —an observation which would lead to the view that the ultimate structure of the bony texture is minutely fibrous.

The finest particles of the earthy substance of bone, obtained by calcination, are described as being minute granules of about $\frac{1}{12000}$ of an inch in diameter.

The marrow exists only in the adult bones; it extends into the cancelli, and even into the larger Haversian canals. In birds, the large respiratory air-cells communicate with air-cavities in most of the larger bones, corresponding with the spaces occupied by marrow in other animals. In order to secure lightness in a similar manner, some of the bones of the head in man and mammalia admit air into their cavities or sinuses.

In the long bones marrow is met with as a yellow mass, consisting principally of fat-cells. In the epiphyses, and in the flat and short bones, the marrow is of a reddish colour and of a softer consistence, and contains, in addition to fat-cells, numerous small contractile nucleated masses of protoplasm. There are also found larger masses of protoplasm, of irregular form, and containing numerous nuclei. These have been termed "*giant cells*," or *myeloplaxes*. The cellular elements of marrow are embedded amongst fine connective tissue.

Bone is one of the partially vascular textures, being pierced everywhere by minute bloodvessels, which pass into the canals of Havers, and its other cavities, so that scarcely any portion of bone, more than $\frac{1}{150}$ of an inch in diameter, is without a bloodvessel. As the greater number of bloodvessels which run into the adjacent portion of bone, previously ramify in the periosteum covering it, the destruction or separation of the periosteum is liable to be followed by the death of the adjacent part of the bone, and the complete destruction of the marrow sometimes induces the same effect, for a like reason, seeing that the bloodvessels of the innermost parts of the bone are connected with those of the medullary membrane.

The arteries and veins, for the most part, run in distinct cavities of the bone; the large principal artery of the medulla, such as that which pierces the shaft of a long bone, is generally called the *nutritious artery.* The veins are numerous and large. Lymphatic vessels and nerves have been traced in small numbers along with bloodvessels, into the interior of the bones.

3. FORMATION AND GROWTH OF BONE.

Bone may be formed in one of two ways:—(1) by ossification in membrane; and (2) by ossification in cartilage. Full details regarding these processes will be found in Quain's Anatomy, vol. II., p. 94 *et seq.*; and it is therefore unnecessary to describe them in this work.

4. CHEMISTRY OF CARTILAGE AND BONE.

Cartilage contains from 54 to 70 per cent. of water, a substance termed *chondrine,* which it yields on prolonged boiling, a small quantity of fat, and from 2 to 3 per cent. of salts. The salts consist of phosphates of lime, and of magnesia, chloride of sodium, carbonate of soda, and sulphates of soda and of potash. It is to be noted that cartilage contains only a very small proportion of salts of potash. Age increases the amount of salts found in cartilage.

The organic basis of bone consists of a substance named *collagene,* which yields *gelatine* on boiling. The salts contained in bone consist chiefly of the tri-basic phosphate of lime, phosphate of magnesia, carbonate of lime, chlorides of sodium and of potassium, and fluoride of calcium. Analysis also yields a small quantity of albumen, fat, and alkaline sulphates, which are probably derived from the bloodvessels and nerves of bone. It is probable that the earthy matter is simply infiltrated into the organic substance of bone, and that it is not in a state of actual chemical combination with it.

The following analyses of bone show its composition in 1000 parts :—

	Femur of man aged 30 years.	Femur. Compact tissue.	Femur. Spongy tissue.
Organic matter,	310·3	314·7	358·2
Mineral matter,	689·7	685·3	641·8
	1000·0	1000·0	1000·0
The mineral matter consisted of—			
Phosphate of lime, Fluoride of calcium,	596·3	582·3	428·2
Carbonate of lime,	73·3	83·5	193·7
Phosphate of magnesia,	13·2	10·3	10·0
Chloride of sodium, &c.,	6·9	9·2	9·9
	689·7	685·3	641·8
The organic matter consisted of—			
Fat,	13·3	314·7	358·2
Collagene,	297·0		
	310·3	314·7	358·2

The long bones of the skeleton are somewhat richer in mineral matter than the others. Phosphate of lime, as the above analysis shows, exists in larger amount in compact than in spongy bone. The bones of herbivora are richer in carbonate of lime than those of carnivora. Salts become more abundant as age advances, so that the bones become more brittle. It has been found possible, by giving food to an animal containing salts of alumina or strontia, to replace part of the lime in bone by one or other of these substances, without altering the structure and general properties of bone.

5. Vital Properties of Cartilage and Bone.

In the healthy state no bloodvessels enter articular cartilages, and they therefore derive their nourishment from the vessels of adjoining textures, more especially from bone, by a process of imbibition. Where cartilage exists in large masses, canals may be formed in its substance for the conveyance of bloodvessels, but cartilage never contains a plexus of capillaries. Cartilage is devoid of sensibility.

The nutrition of bone, even in the adult, is active, as is shown by the morphological changes which it may undergo in the course of disease. The bones are well supplied with bloodvessels, which are derived partly from periosteal vessels, and partly from vessels in the medullary canal. Fine vessels run through all parts of the compact tissue in the Haversian canals. From these nutritious fluid permeates the substance of the bone, in all probability by the canaliculi uniting the masses of protoplasm in the lacunæ.

Bone in the healthy condition is only feebly sensitive; but when inflamed, especially near the periosteal surface, it may become acutely painful.

Cartilage forms the framework of the skeleton of the embryo, and gradually is replaced by bone until only the permanent cartilages are left. These form smooth surfaces in the joints, and thus allow the various parts of the skeleton to move on each other with a minimum of friction, while, by their consistence and elasticity, they break the force of concussion, and utilize energy in the most effective manner. Certain of the permanent cartilages also enter into the formation of the external ear, the nose, the eyelids, the Eustachian tube, the larynx, and the windpipe, maintaining the form of these organs, and giving attachment to muscles and ligaments.

Bones in the adult form the framework of the skeleton. Some may be regarded as the passive organs of locomotion, while others form, with the soft parts, the cavities of the body, and also serve as protective structures for delicate organs.

As to structure and general properties of Cartilage, consult SHARPEY and SCHÄFER in Quain's Anat., Vol. II., p. 72. ROLLETT, in STRICKER'S Human and Comparative Physiology, Vol. I., p. 96. KLEIN, in Handbook for the Physiological Laboratory, p. 46. As to effects of electricity on cartilage cells, see ROLLETT, *ut supra;* and for a more detailed account, HEIDENHAIN, Studien des Physiologischen Instituts zu Breslau, Heft 2, Leipzig, 1863, p. 1. As to the effects of irritation on cartilage causing inflammatory changes, see REDFERN'S original paper, Monthly Journal of the Medical Sciences, 1850. Regarding structure and development of bone, consult TOMES' Art. "Osseous Tissue," in the Cyclop. of Anat. and Physiol.; TOMES' and DE MORGAN, Phil. Trans., 1853, part I., p. 109; SHARPEY and SCHÄFER, Quain's Anat. p. 79; ROLLETT, *ut supra*, p. 115. As to marrow, consult ROBIN, Journal de l'Anatomie et de la Physiologie, 1864, p. 88.

VI.—THE NERVOUS TISSUES.

The nervous system, considered with a view to its functions, may be regarded as consisting of three sets of organs acting in a different manner: the first *central*, the second *peripheral*, and the third *intermediate*. The first consists of various forms of *nerve cells;* the second of certain structures termed *terminal organs*, which exist in the organs of special sense, the muscles, and perhaps in the walls of bloodvessels and in the ultimate structures of glands; and the third, of *nerves*, which are cords distributed through the various organs of the body, and which perform a function chiefly, if not solely, of a communicating or internuncial kind. The nerve cells are aggregated in certain parts of the body into masses, forming the cerebro-spinal axis and various ganglia, the special functions of which, as well as those of the terminal organs, will be described in treating of the nervous system and senses. Here, however, we will describe the general properties of nervous tissue, and also a few of the simpler forms of nervous action, which the student ought to be acquainted with at this early period of his studies.

1. Structure of Nervous Tissue.

a. *Nerve Cells.*

Nerve cells are the essential parts of the central nervous organs and of ganglia. They consist of cells formed of finely-granular protoplasm containing a nucleus. They vary much in form and size. The existence of a cell wall is doubtful. Almost all are furnished with prolongations which are continuous with nerve fibres. These prolongations are termed *poles*, and according to the number in connection with a cell, it is termed unipolar, bi-polar, tripolar, and multipolar. Some cells appear to be a-polar, but it is very probable that in these cases the fragile poles have been torn away in the course of preparation. Each multipolar nerve cell possesses (1) a process which is directly continuous with the central part, termed the axis-cylinder, of a nerve fibre; and (2) of several more slender protoplasmic processes which are also continuous with the axis-cylinders of smaller nerves. The following general facts may be noted:—

1. *A-polar* nerve cells are found in ganglia, such as the Gasserian ganglion and the sympathetic ganglia.
2. *Unipolar* nerve cells are probably never met with. Sometimes the large cells found at the margin of the granular layer of the cerebellum are described as such, but these have in reality two poles.

3. *Bi-polar* nerve cells are formed in the ganglia on the posterior roots of the spinal nerves, and may be well seen in the skate. (*Allen Thomson.*)
4. *Tri-polar* nerve cells are usually mentioned as existing in the deeper layers of the grey matter of cerebral convolutions; but such cells are better described as *pyramidal*, having a pole issuing from each angle of the pyramid, and another from the centre of its base.
5. *Multipolar* nerve cells are characteristic of the grey matter of the spinal cord.
6. Cells having two fibres in connection with them, one of which is coiled spirally round the other, have been described by Lionel Beale and J. Arnold.

In the central nervous masses the cells lie amongst a stroma of very delicate connective tissue termed *neuroglia.*

b. *Nerve Fibres.*

Nerve fibres exist in the nerve trunks and their ramifications, of which they form the essential part, and in nerve centres and ganglia, where they are in connection with nerve cells. The nerve fibres, in the fresh condition, present the appearance of a homogeneous mass, strongly refracting light, and contained in a translucent membrane. After death, and under the influence of certain re-agents, an ultimate nerve fibre presents the following parts:—(1) a delicate and perfectly transparent sheath, within which there is (2) a cylinder composed of perfectly transparent, highly refractive matter, termed the *white substance of Schwann.* Lastly (3) there is in the centre of the nerve fibre a rod of semi-fluid matter, termed the *axis-cylinder.* The axis-cylinder coagulates after death, or on the addition of various re-agents, when it may be described as a fibre, but it is important to notice that during life both it and the white substance surrounding it are in a semi-fluid condition. Ranvier has demonstrated, by the use of a solution of perosmic acid, OsO_4, which, under the influence of light, blackens the white substance, that the white substance is interrupted at regular intervals, whilst the axis-cylinder is continuous. These interruptions are known as the *nodes* of Ranvier. Delicate nerve fibres, such as are found in the grey matter of the cerebral convolutions, have no white substance. When nerve fibres, such as those just described, are seen in the fresh condition by transmitted light, they present the appearance of a double contour; that is, two delicate lines on each side of a clear band. This appearance is characteristic of the great majority of nerve fibres found in the cerebro-spinal centres, and in ordinary nerves. In the nerves and ganglia of the sympathetic system, however, the fibres do not present the double contour, and they appear to be flattened bands, having nuclei in their substance at irregular intervals. Such fibres are sometimes termed *non-medullated*, or the fibres of Remak, after their discoverer.

The most important part of the nerve fibre, so far as conduction is concerned, is the axis-cylinder; which, as already stated, is continuous with the poles or processes of nerve cells. The application of certain chemical re-agents, such as nitrate of silver and chloride of gold, is sometimes followed by the appearance of longitudinal striæ in the axis-cylinder, indicating that possibly it may be composed of a large number of extremely delicate fibres.

Nerves visible to the naked eye consist of varying numbers of nerve fibres, bound together by a delicate sheath of connective tissue, which may send septæ inwards, so as to divide the fibres into groups. The sheath of connective tissue is sometimes termed the *neurilemma.* When a transverse section of a nerve, stained with carmine, is examined with a magnifying power of 500 diameters, it is easy to observe that it is composed of nerve fibres of different diameters, and that these are arranged in bundles.

c. *Terminal Organs.*

These are structures of various forms, according to the organ in which they are found. As examples, the following may be mentioned :—the end-plates in voluntary muscle; the touch-bodies of various kinds found in the skin; the taste-bodies found in the tongue; the apparatus in the nasal passages, connected with the olfactory nerve; the rods and cones of the retina; and the hair-like processes found in the internal ear. A description of the minute structure of these organs will be given in treating of the physiology of the senses.

2. CHEMISTRY OF NERVOUS TISSUE.

It is manifestly almost impossible to obtain a chemical analysis of nerve cells, apart from nerve fibres and connective tissue. Consequently, our knowledge of the chemistry of nervous tissue is still very imperfect. Nervous tissue contains a considerable quantity of fatty matter, and fat also exists in the white substance of Schwann. The reaction of living nervous tissue is neutral, but it becomes acid after death. It has been found that the chemical composition of nerves resembles that of masses of cerebral matter, of which the following table shows roughly the composition in 100 parts :—

	Grey matter (nerve cells).		White matter (nerve fibres).
Water, ...	81·6	...	68·3
Solids, ...	18·4	...	31·7
	100·0	...	100·0

In 100 parts of perfectly dry cerebral matter :—

	Grey matter.	White matter.
Albuminoids,	55·6	24·7
Lecithine,.	17·2	9·9
Cholestrine and fats,	18·6	52·1
Cerebrine,	0·5	9·5
Substances insoluble in ether,	6·7	3·3
Salts,	1·4	0·5
	100·0	100·0

The salts found in nervous matter are similar to those in blood, and it is remarkable to observe the large amounts of phosphates and of potash. The following analysis has been given of 100 parts of the salts obtained from cerebral matter :—

Potash,	32·42	Phosphoric acid in combination,	39·02
Soda,	10·69	Free phosphoric acid,	8·78
Magnesia,	1·23	Sulphuric acid,	0·75
Lime,	0·72	Silica,	0·42
Chloride of sodium,	4·74		
Phosphate of iron,	1·23		

Total = 100.

Nervous matter has also yielded to the chemist many nitrogenous derivatives, such as creatine, creatinine, leucine, xanthine, urea, uric acid, &c. The student should contrast the composition of white with grey matter.

3. Physical Properties of Nervous Tissue.

a. *General Properties.*

Grey matter is soft and diffluent. The white matter, even in nerves, presents little consistence or cohesion, and what it has is probably due to the connective tissue it contains. The elasticity of nerves is very imperfect. White matter, consisting entirely of nerve fibres, according to Ranke, absorbs fluids containing different saline substances at very different rates. Thus, chloride of sodium is not absorbed at all, sulphate of soda is absorbed only in small amount, while the acid phosphate of soda and the salts of potash are absorbed with avidity.

b. *Production of Heat.*

Valentine has observed a constant production of heat during the state of activity of a nerve. It is of such small amount as to be scarcely perceptible even with the most delicate thermo-electric appliances.

c. *Electrical Properties.*

When a portion of living nerve is placed on the cushions of the galvanometer, in the manner already described with reference to muscle, so that the transverse section touches one cushion, whilst the longitudinal surface touches the other, a current passes through the circuit of the galvanometer from the longitudinal surface to the transverse section, and when a nerve is excited to action, there is a negative variation of this current. It will be observed that the phenomena are precisely the same as in the case of muscle.

4. Vital Properties of Nervous Tissue.

a. *Nutrition.*

Grey matter, consisting of nerve cells, has always a greater supply of blood than white matter, as indicated by the richness of the capillary network. Nerve cells derive their nourishment from plasma transuding from the capillaries, but it is important to note that the nutrition of the nerve cell influences that of the nerve fibres with which it is connected. It was shown by Waller that when a nerve is separated from its trophic nerve centre, such as the grey matter of the spinal cord for the motor roots, and the ganglia on the posterior root for the sensory roots, the end of the nerve separated from the centre undergoes fatty degeneration. This degeneration may affect not only the whole nerve, but even the end-plates in a muscle. These phenomena, which commence in warm-blooded animals on the fourth day after the operation, and much later in cold-blooded animals, are grouped under the general name of the *Law of Waller.*

According to Ranvier, nerve fibres lie in lymphatic spaces, and the plasma containing nutritive materials reaches the axis cylinder at the points where the white substance of Schwann is deficient,—the nodes of Ranvier above mentioned.

Active nerve substance absorbs oxygen and eliminates carbonic acid. The chemical substances which may be produced by the decomposition of nervous matter during a state of activity are quite unknown.

When a nerve is cut in a mammal, the ends may reunite so completely as to ensure a return of the normal function of the nerve in from two to five weeks. Surgeons have frequently observed a return of sensibility to a part some time after section of the nerve supplying it, a fact which may be explained either by reunion of the nerve or by the establishment of new routes of transmission through anastomosing fibres.

b. *Nervous Excitability.*

When a nerve is irritated in any part of its course, a condition is excited in its fibres which is transmitted along the fibres with a certain velocity, and which may produce ultimate effects of various kinds, depending upon the nature of the structures at the end of the fibres. This property of responding to a stimulus is termed *excitability,* and the property of the nerve by which a change excited in it is conveyed towards its extremities is known as *conductivity*. As just stated, the phenomena following stimulation of a nerve may be of various kinds. Thus there may be *contraction* of a muscle if the nerve terminates in a muscle; change of the *calibre* of a bloodvessel if the nerve ends in that structure; *secretion* from a gland if the nerve is in connection either with the vessels or the nerve cells of the gland; and a *feeling* of pain or of pleasure if the nerve fibres go to a sentient brain. In all of these instances, the nature of the change in the nerve and the mode of its transmission is the same, and the results are different because the nerves terminate in different kinds of structure.

The intimate nature of the change in a nerve fibre effected by a stimulus is quite unknown; but it is important to appreciate clearly that a nerve is both a *receiver* and a *conductor* of impressions. It is impossible at present to say whether an influence transmitted along a nerve is analogous to the passage of electricity along a conductor, or to a rapid passage onwards from the point of stimulation of some form of chemical action or isomeric transformation. We only know the fact, and it is more philosophical to examine the conditions of nervous action than to speculate regarding its exact mechanism.

One of the conditions of nervous excitability is that there be periods of repose and of activity. A high state of activity, though lasting only for a short time, and prolonged activity, soon produce a feeling of fatigue, and if too long continued, may abolish excitability altogether. On the other hand, a lengthened period of absolute rest lowers excitability, and if this state be continued too long, there may be wasting and degeneration of the nerve.

Heat up to a certain temperature, which varies in different species of animals, augments, while cold diminishes, excitability. A deficient supply of blood, as when the main artery of a limb is ligatured, is quickly followed by a fall of excitability. Slight drying increases excitability, as may be frequently seen in the nerve-muscle preparation used in physiological experiments. Potash, potash salts, the acids, &c., abolish, whilst a weak solution of common salt conserves, excitability. According to Eckhard, it is independent of oxygen.

When a nerve is divided from the nerve centres, excitability disappears from it progressively from the section towards the termination of the nerve, but in each successive segment the disappearance of excitability is preceded by a period of exaggeration.

Nerves may be excited by various kinds of stimuli. The normal stimulus arises either from nerve cells in the great centres, or perhaps in ganglia, or from the terminal organs, or from delicate impressions made directly on the nerve in such surfaces as the skin and mucous membranes. Nerves may also be excited *mechanically*, as by pressure, beating, section, pricking, &c.; *electrically*, by the application of continuous or induced currents; *thermally*, by variation of temperature; or *chemically*, by such substances as acids, alkalies, metallic salts, &c. It is to be observed, however, that whatever may be the nature of the stimulus, the result in the case of a particular nerve will always be the same. Thus any kind of interrupted stimulus applied to a motor nerve, if of sufficient intensity and lasting for a sufficient length of time, will always produce tetanus. The special effect of electricity on nerves will be better appreciated after discussing the facts regarding the conductivity of nerve.

c. *Nervous Conductivity.*

When a change is produced at one point of a nerve by a stimulus, it travels along the nerve with a certain rapidity. This transmission is sometimes called the *nerve current.*

The velocity of the nerve current in a *motor* nerve was first determined by Helmholtz. Various methods of measurement have been adopted by physiologists from time to time; but the general principle of all the methods is to cause a muscle to contract by successively irritating two points of a nerve more or less distant from the muscle, and to obtain a record of the contracting muscle upon a rapidly-moving surface. It is evident that the distance between the two points at which the two curves leave the horizontal line will indicate the length of time the nerve current took in passing from the stimulated point at a distance from the muscle to the

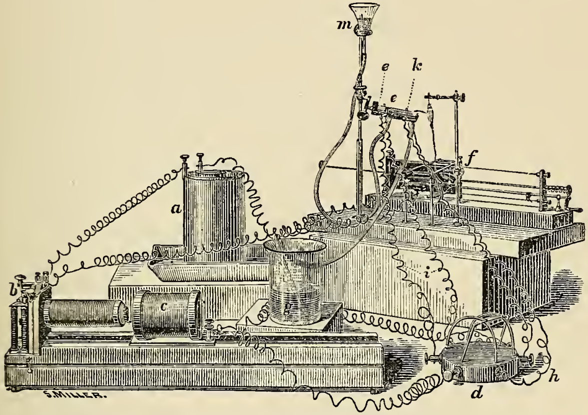


FIG. 36.—Arrangement of apparatus for measuring the rapidity of the nerve current. *a*, Daniel's element; *b*, primary coil of induction machine; *c*, secondary coil; *d*, Pohl's commutator for directing the induction shock either along the wires *h* or the wires *i* to the electrodes in the vulcanite box *e* at *e* or *k*. This part of the apparatus is also seen in Fig. 17, VII and VIII. *f*, spring myograph, consisting of smoked-glass plate, which is driven in front of the stylet by the recoil of the spring seen to the right of the apparatus. Above the lever of the myograph the muscle is secured by fixing the lower end of the femur in the brass forceps, and the nerve is stretched across the electrodes *e*. These electrodes consist of an elongated vulcanite box into which platinum wires are fixed at *e* and *k*. The roof of the box is formed of a copper plate, and through it, from the funnel *m*, either hot or cold water may be allowed to flow through an indiarubber tube to the beaker *g*. The latter arrangement is for the purpose of subjecting the nerve to different temperatures.

other stimulated point close to the muscle. A convenient arrangement for making the experiment is shown in Fig. 36, in which the spring myograph of Du Bois-Reymond is employed.

This apparatus, which is also seen in Fig. 11, p. 94, consists of a smoked-glass plate which is driven in front of the recording stylet of the myograph by the recoil of a steel spring. Underneath the frame carrying the glass plate there are two binding screws, to one of which is attached a rectangular arm of brass, which can so move horizontally as to establish metallic connection between the two binding screws. By means of these binding screws the myograph is interposed in the circuit of the galvanic element *a* and the primary coil of the induction machine *b*, and the arm of brass above mentioned is so placed as to connect both binding screws, and thus complete the circuit. From underneath the frame carrying the smoked-glass plate there descends a small flange, which (when the glass plate, by releasing a catch seen at the left end of the plate in the figure, passes from left to right) pushes the brass arm aside, and thus interrupts the circuit of the primary coil. When this occurs, an opening shock is transmitted from the secondary coil *c* to the commutator *d*. By means of the commutator the secondary shock may be transmitted to the nerve, either to a point close to the muscle *k*, or at a distance from it, *e*. Suppose the apparatus had been so arranged, by dipping

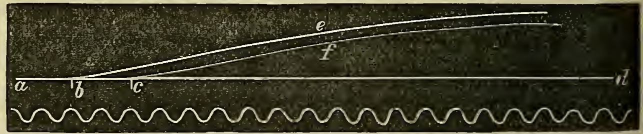


Fig. 37.—Tracing obtained on the smoked-glass surface of the spring myograph in the experiment for determining the rapidity of the nerve current. Chronograph = 200 vibrations per second.

the wires of the commutator *d* into the mercury troughs, as to send the shock to the nerve at a point close to the muscle *k;* the muscle thus stimulated contracts, and draws on the smoked surface of the glass the curve in Fig. 37. This curve leaves the horizontal line *a b c d*, which would be drawn by the muscle at rest, at *b*. Arrangements are then made for another experiment in which the nerve will be stimulated at a distance from the muscle at the point *e* in Fig. 36. This is done by again placing the smoked-glass plate in the position seen in the figure, closing the primary circuit by the brass arm at the binding screws as already described, and reversing the commutator so as to send the shock along the wires *i*, Fig. 36. The muscle again contracts when the primary circuit is opened, and this time it describes on the smoked surface the curve *c f*, Fig. 37. It will be observed that this curve leaves the horizontal line at *c*, that is, a little later than when the nerve was stimulated close to the muscle. It follows, therefore, that the distance on the horizontal line from *b* to *c* represents the time occupied by the transmission of the nervous impulse from *e* to *k* (Fig. 36)—the time required for the passage of the current along the portion of the nerve between *k* and the muscle, and the period of latent stimulation of the muscle, being the same in both experiments. A chronographic tracing on the smoked surface will measure this time, and the length of the portion of the nerve can be readily ascertained. It will then be found that in the case of the motor nerves of the frog nervous transmission is at the rate of about 75 to 90 feet (26 to 27 metres) per second. Helmholtz and Baxt, by independent methods, in which the contractions of the adductor muscles of the thumb were recorded after stimulation of two different points on the radial nerve, have determined the rate of transmission in the motor nerves of the living man to be about 100 to 120 feet per second. Some have found the rate so high as 200 feet per second.

The rate of transmission in *sensory* nerves may be measured in the following manner: On exciting a point of the skin, say on the great toe of the person who is the subject of the experiment, he makes a signal that he perceives the sensation; the moment of excitation and the signal are recorded on a rapidly-moving surface, and the interval is measured; another experiment is then made by exciting the skin at a point nearer the nerve centres, say at the upper part of the thigh; the difference of the two measures will give the rapidity of sensitive transmission, supposing the time occupied by perception, volition, the transmission of the impulse along the motor nerves to the muscles of the arm which makes the signal, and by the contraction of the muscles themselves, is the same in both experiments. It will be seen that in such a method there are apparent sources of fallacy, but it is remarkable that most observers have found the rapidity to be very nearly the same as that of motor nerves—namely, about 110 to 120 feet per second.

Nervous transmission is very much slower than the transmission of electricity along a conductor. It is increased by heat and diminished by cold.

There are still several points of interest connected with nervous conductivity.

a. When some of the fibres in a nerve are stimulated, the transmission is not communicated to neighbouring fibres. Some have supposed that the white substance of Schwann serves as an insulator to the conducting axis cylinder. Of this, however, there is no proof; and there is the further difficulty in accepting this view, that many of the minute nerve fibres in the cerebro-spinal centres and the fibres of the sympathetic system are devoid of white substance.

b. Nervous transmission is apparently the same process both in sensory and in motor nerves, and, as before explained, the result depends on the nature of the apparatus at the end of the nerve.

c. At one time it was generally held that motor and sensory nerves could convey impressions only in one direction—motor nerves towards a muscle, and sensory nerves towards a ganglion or nerve centre. When we consider, however, that the structure of both kinds of nerves is apparently identical, and that the semi-fluid condition of the matter in a fibre would appear to favour the transmission of a vibration equally in both directions, just as occurs on tapping the middle of a long indiarubber tube filled with water or air, the presumption is in favour of transmission in both directions. This view is supported, in addition, by the following observations: (1) When a nerve is stimulated electrically at one point, a disturbance of the electrical state of the nerve may be detected by a galvanometer for a considerable distance in both directions; and (2) actual experiments by Vulpian and Paul Bert, in which they divided contiguous motor and sensory nerves, and afterwards promoted their reunion in such a manner that the central end of what was formerly a sensory nerve was joined to the distal end of what was formerly a motor nerve, and *vice versa*, have shown that after a certain time transmission occurred in a normal manner. It is evident, however, that the risks of fallacy in such difficult experiments are so great as not to warrant us in placing implicit confidence in the interpretations given of the results.

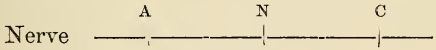
5. Electrical Stimulation of Nerve.

A continuous current of electricity, of moderate intensity, produces under ordinary circumstances no evident effect upon a motor nerve connected with a muscle, except at the moment it enters the nerve and the moment it quits it, or in other words there is a contraction of the muscle only at the moments of opening and closing the current. During the passage of the current no effect is produced. In the case of a sensory nerve, the current acts with more energy on entering than on leaving the nerve; but even during the passage of the current, a feeble sensation may be experienced.

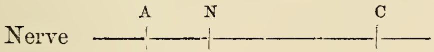
The effect on a nerve of opening and closing continuous currents depends (1) on the intensity, and (2) on the direction of the current.

An interrupted galvanic current transmitted along a nerve weakens, and if too long continued destroys the nerve current and the excitability of the nerve. But if a constant galvanic stream be sent along a portion of nerve, it is thrown into a peculiar condition, called by Du Bois-Reymond the *electrotonic state* (ἤλεκτρον, electricity; τόνος, tension). This term was first used by Faraday to describe the peculiar molecular condition of a wire traversed by a current of electricity. If the constant stream pass in the natural direction of the normal nerve current, the latter is augmented; if in the contrary direction, it is diminished. While a portion of the nerve is in an electrotonic state, it may be shown experimentally, that its physiological action has undergone certain modifications. For the sake of clearness, we shall subdivide the physiological action of the nerve as follows: (1) its electro-motive force; (2) its conductivity, or power of conducting the influence of impressions; and (3) its excitability; that is, the property of nerve in virtue of which it is capable of receiving impressions and generating an influence.

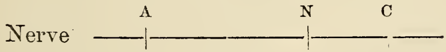
While a portion of nerve is traversed by a constant current, it is found that its physiological properties are altered so that it may be divided by a neutral point, situated between the two poles, into two portions. The portion in the neighbourhood of the positive pole is termed the anelectrotonic portion (ἄνω, upwards; ἤλεκτρον, electricity; and τόνος, tension), while that in the neighbourhood of the negative pole is termed the cathelectrotonic portion (κατὰ, downwards; ἤλεκτρον, electricity; and τόνος, tension). The anelectrotonic portion extends for some distance outside the positive pole, and the cathelectrotonic portion for some distance outside the negative pole. The position of the neutral point, or *point of indifference*, that is the point where the nerve is neither in a cathelectrotonic, nor in an anelectrotonic state, and the extent of the cathelectrotonic and anelectrotonic portions is determined by the strength of the current transmitted through the nerve. With a current of *medium* strength, the neutral point is exactly midway between the two poles, and the two portions are equal in extent, as will be seen in the following diagram, in which A is the anelectrotonic, C the cathelectrotonic portion, and N the point of indifference.



With a weak current, the neutral point is nearer to the positive than to the negative pole, and the greater portion of the nerve is in a cathelectrotonic condition. Thus:—



With a strong current, the neutral point is nearer to the negative than to the positive pole, and the greater portion of the nerve is in an anelectrotonic condition. Thus:—



Of course, intermediate strengths of the current will produce intermediate positions of the neutral point.

Pflüger discovered that under these circumstances the excitability and conductivity of the nerve are diminished in the neighbourhood of the *positive* pole, while its electro-motive force is increased; but the excitability and conductivity of the nerve are increased in the neighbourhood of the *negative* pole, while its electric power is diminished. In other words, when a portion of nerve is in the anelectrotonic condition, its power of receiving impressions is diminished, it does not conduct nervous force so rapidly, but it evolves more electricity than it would do in the normal state The reverse is the case when a portion of nerve is in the cathelectrotonic state. It is then more excitable, conducts nervous force more rapidly, but its power of evolving electricity is diminished.

These results may be impressed on the memory by the aid of the following table:—

State of Nerve.	Functions of Nerve.		
	Electro-motive Force.	Conductivity.	Excitability.
Anelectrotonous, .	Increased.	Diminished.	Diminished.
Cathelectrotonous, .	Diminished.	Increased.	Increased.

Pflüger's Law of Contraction.—By the law of contraction is meant all the actions which a muscle exhibits on opening or closing a current, varying in strength and direction, passing through its nerve. Many of the earliest experimenters in electro-physiology were struck by the fact, often observed, that a *feeble* current of electricity, acting on a nerve, will cause contraction in a muscle, when a *strong* current fails to do so. It was also observed that while a constant current was flowing through a portion of nerve attached to a muscle, the muscle contracted *only on opening and closing the current*, and not during the passage of the current. But the muscle sometimes contracted, sometimes it did not. Numerous experiments made by Du Bois Reymond, Eckhard, Pfaff, Ritter, Nobili, Pflüger, Schiff, Wundt, Cl. Bernard, Fick, and C. Bland Radcliffe, have shown that the phenomenon of the contraction of the muscle is influenced, *first*, by the direction, and, *second*, by the strength of the current sent through the nerve. In the description of these phenomena, physiologists have made use of certain terms it is necessary to explain. When the current is transmitted from the muscle in the direction of the spinal cord, the current is called an *upward*, or *centripetal* current; when from the cord in the direction of the muscle, it is called a *downward* and *outward* or *centrifugal* current. When the current is derived from only one of Grove's cells, the strength of the current is described as *weak;* when from two or three of Grove's cells, as *medium;* and when from five or six of Grove's cells, as *strong.* In these experiments, small elements or cells are employed, and an instrument, termed a rheocord, for further regulating the strength of the current, is introduced into the circuit. By means of Du Bois-Reymond's key, (Fig. 17, vi), the current may be opened or closed at pleasure. It is broken or interrupted when the key is *opened*, and is again allowed to pass onwards when the key is *closed.*

The following table shows the results of Pflüger's experiments, which are summarily expressed as *Pflüger's law of contraction*, though it is really a statement of facts, to explain which Pflüger has formulated a law called the *law of stimulation*:—

Current Strength.	Upward Current.		Downward Current.	
Weak.	Close.	Contraction.	Close.	Rest.
	Open.	Rest.	Open.	Strong contraction.
Medium.	Close.	Strong contraction.	Close.	Strong contraction.
	Open.	Strong contraction.	Open.	Strong contraction.
Strong.	Close.	Rest.	Close.	Strong contraction.
	Open.	Very strong contraction.	Open.	Rest, or feeble contraction.

On beginning with an exceedingly feeble upward current, neither opening nor closing gives rise to contraction; but, by increasing the strength of the current gradually, we invariably get contraction first on closing, but opening has no effect. By gradually strengthening the current, we at length reach a point when there is contraction both on opening and closing. By and bye, when a certain maximum is reached, the closing contraction becomes weaker, and finally disappears when the current becomes strong. Similar results are to be got with a downward current, except that the contraction with a weak current first appears, according to many experimenters, on opening, and not on closing, and that there is contraction on closing, and none, or a very feeble contraction, on opening a strong current. Pflüger, however, found that with a weak downward current he obtained contraction on closing and rest on opening, a result in accordance with the theory of stimulation he has offered.

Pflüger's Law of Stimulation.—To explain these phenomena, Pflüger has propounded the following law: "*A given piece of nerve is stimulated only by the appearance of cathelectrotonous and the disappearance of anelectrotonous, but the disappearance of cathelectrotonous and the appearance of anelectrotonous has no effect.*" In other words, when a current is closed, the nerve is stimulated by the passage of the nerve near the negative pole, from a normal into a cathelectrotonic state; but, when a current is opened, the nerve is stimulated by the passage of the nerve near the positive pole from an anelectrotonic into a normal state.

Pflüger's theory of stimulation affords a satisfactory explanation of the results given in the table already quoted; and it also explains why a feeble current causes contraction more strongly than a powerful one. This will be evident, if we apply it to the individual instances by the aid of the following diagrams, in which M = muscle, N nerve, – negative pole, and + the positive pole of the electrodes, the arrow the direction of the current, and PI the point of indifference :—

1st. *Feeble Upward Current.—Closed*, contraction; *opened*, rest. (Diagram I.) Here the point of indifference is near the positive pole; and, consequently, the cathelectrotonic area is extensive. When the current is closed, the nerve is stimulated by the establishment of cathelectrotonus in the portion *a*, in which the excitability of the nerve is increased, and a contraction of the muscle is the result. On the other hand, on opening the current, a small portion of the nerve, in the neighbourhood of the positive pole *b*, passes from the anelectrotonic into the normal state, and the nerve is stimulated; but the excitability of the nerve being much lowered, the stimulus is so weak that the muscle does not contract.

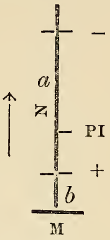


Diagram I.

2nd. *Feeble Downward Current.—Closed*, contraction; *opened*, rest (Pflüger). (Diagram II.) On closing, a large portion of the nerve next the muscle *a*, passes into the cathelectrotonic state, the nerve is stimulated, and contraction of the muscle is the result; but, on opening, a small portion of the nerve, at a distance from the muscle *b*, passes from the anelectrotonic state, and the stimulation is so weak that the muscle does not contract. But, as already mentioned, p. 168, many physiologists have contraction only on opening, and none on closing, a result which is not explained by Pflüger's law. The discrepancy probably arises from the great difficulty in graduating the strength of the current.

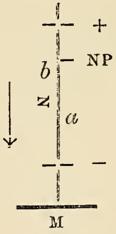


Diagram II.

3rd and 4th. *Medium Upward and Downward Current.—Closed*, contraction; *opened*, contraction. In this instance, the neutral point being midway between the two poles, the anelectrotonic and cathelectrotonic areas are equal in extent. (Diagram III.)

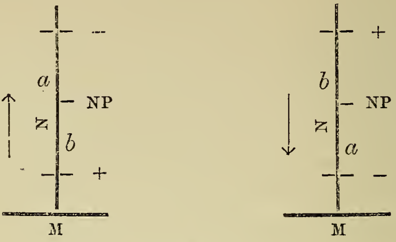


Diagram III.

On both opening and closing there is a strong contraction, because both anelectrotonus and cathelectrotonus increase with the current strength; and with the increase in the extent of the anelectrotonic portion *b*, there is also an opening contraction. On closing, the nerve is stimulated in the neighbourhood of the negative pole *a*, by the establishment of cathelectrotonus; and, on opening, the nerve is stimulated in the neighbourhood of the positive pole *b*, by the disappearance of anelectrotonus.

5th. *Strong Upward Current.—Closed*, rest; *opened*, contraction. (Diagram IV.) In this instance the neutral point is near the negative pole, and the cathelectrotonic area is much smaller than the anelectrotonic. On closing, the smaller portion, *a*, passes into the cathelectrotonic state; the nerve is stimulated, but, as the stimulation has not sufficient power to travel along the anelectrotonic portion, *b*, in which the conductivity is much diminished, there is no contraction of the muscle. On opening, the portion *b* passes from the anelectrotonic into the normal state, the nerve is stimulated thereby, and the muscle contracts.

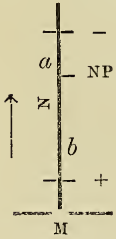


Diagram IV.

6th. *Strong Downward Current.—Closed,* contraction; *opened,* rest or feeble contraction. (Diagram V.) The closing contraction in this case is caused by the formation of the cathelectrotonus in the portion of the nerve *a*, next to the muscle. But, on opening the current, there is usually no contraction of the muscle, or at best a very feeble contraction, because the stimulation arising from the passage of the portion *b* from the anelectrotonic to the normal state, cannot reach the muscle, owing to the existence in the portion *a* of a peculiar molecular state greatly diminishing its conductivity, termed by Pflüger the *negative modification.*

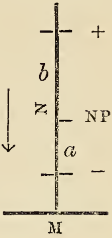


Diagram V.

Another important law, discovered by Pflüger, may be thus expressed, namely: *The further a nerve is irritated from the muscle, the greater is the excitability of the one, and the contraction of the other.* Two theories have been advanced in explanation. One supposes that the molecules throughout the nerve possess a certain amount of tonic force, a part of which is given off during the transmission of the influence, so that, as the current progresses, it receives accumulated intensity, like an avalanche as it rushes down a precipice. The other theory supposes that a motor nerve becomes more excitable the nearer it approaches the nervous centre of its origin, so that an irritant produces a more marked effect when applied there than at a distance.

It must be obvious that the knowledge of the facts now referred to, regarding the varied effects produced in muscles by the strength, direction, and position of the applied current, must be of the greatest importance to the medical man in his endeavours to employ electricity as a therapeutic agent in the treatment of paralysis, neuralgia, and other nervous diseases.

6. Functions of Nerve Cells and of Grey Matter.

The usual stimuli which excite activity in nerve cells are the impressions transmitted from the periphery along sensory nerves or influences sent from cell to cell by intermediate nerves. Thus, when an impression is made on a sensory nerve in the skin, the influence travels to certain nerve cells in the brain, by the activity of which there is, under ordinary circumstances, perception of the impression. Again, the influence may pass to certain nerve cells in the spinal cord and may be transmitted by them along other nerve fibres to another group of cells, in another part of the cerebro-spinal axis, or it may be directly reflected along other fibres to muscles so as to cause contractions. For the manifestation of this kind of activity a due supply and a proper quality of blood is required. If the supply of blood to nerve cells be suddenly cut off, they may manifest unusual activity for a short time, as in the sudden nervous discharges which cause the convulsions seen after severe hæmorrhage, but the activity of the cells, especially in warm-blooded animals, quickly disappears. The presence in the blood of various substances, such as excess of carbonic acid or of certain poisons, may also be followed by symptoms of direct excitation of nerve cells.

When nerve cells are excited by a single instantaneous stimulus, they respond in an appreciably short interval of time; but if the stimulus be repeated at short intervals, there are successive and very brief discharges of nervous energy, separated by intervals of rest. Thus we have seen that the voluntary contraction of a muscle is caused by a rapid series of nervous discharges transmitted along a motor nerve, and that the individual and partial contractions produced by these are fused together so as to form a single muscular contraction. But if, from the changes in structure which are frequently the result of age, or from the effects of alcohol or other active substance, the discharges from the nerve centre become intermittent or have longer periods of repose than usual, the muscles tremble, and sometimes even the individual contractions may be noticed. It is probable that intermittent discharges from nerve cells are connected with the rhythmic movements of the heart and of the respiratory apparatus.

The activity of nerve cells may or may not be associated with consciousness. In the ganglia found in many organs, which act as local centres, in the spinal cord, in all the parts of the encephalon, with the exception of certain portions of the cerebrum, their activity is automatic and unconscious; but in the cerebrum their modifications are associated with or produce states of conscious feeling. In all probability, however, the kind of modification may be the same both in conscious and in unconscious activity of cells, as we find that many movements, the results of nervous activity, which are at first effected by conscious effort, become, after long repetition, unconscious actions. As examples, we have the power of locomotion and of maintaining equilibrium developed from infancy to adult life, and the rapid movements of the fingers of the pianist or violonist, at first acquired by laborious effort, but afterwards performed unconsciously.

7. GENERAL PHENOMENA OF NERVOUS ACTIVITY.

It will assist the student materially if at this stage of his physiological studies he acquires a general notion of some of the principal varieties of nervous activity. Without this preliminary knowledge, he would find it difficult to understand any account of the influence which the nervous system exerts on such important functions as digestion, circulation, and respiration. A short description of these will therefore be given here, leaving a detailed account of the functions of central nervous organs and of the cranial and spinal nerves to a later stage.

a. *Nerves.*

Functionally, nerve fibres may be divided into five groups—motor, sensory, vascular, secretory, and inhibitory.

The original meaning attached to the term *motor nerve* was a nerve entirely composed of fibres by the excitation of which influences were conveyed to a muscle which caused the muscle to contract. As these influences passed outwards from a nerve centre towards the periphery of the body, they were also termed *efferent* nerves. On the other hand, nerves were found which, when stimulated, gave rise to sensations of pleasure or of pain, and these were called *sensory* nerves. Finally, it was shown that a third class of nerves were composed both of sensory and of motor fibres, and they were called *senso-motor* nerves. Sensory nerves were also subdivided into those of general and those of special sensibility. This was an artificial classification, based on the fact that when a nerve of so-called special sensation, such as the optic, was stimulated in any way whatever, the same kind of sensation followed. Thus, stimulation of the optic nerve by cutting, pricking, or by pressure or electricity, is always followed by a luminous sensation. The other nerves of special sensation were the auditory, gustatory, olfactory, and tactile, and the remainder, distributed to the muscles and visceral organs, were supposed to convey influences to the cerebral centres, which gave rise to obscure and vague sensations, such as those of the state of the muscles in fatigue, and of general bodily discomfort or satisfaction. It is equally true as regards these nerves, that in whatever way they are excited, the same kind of sensation is experienced. Anatomically, nerves are still classified on this basis.

But the progress of research showed that when certain nerve fibres were stimulated, the result was not necessarily always a muscular contraction, but it might be contraction of the calibre of a bloodvessel, increased secretion from a gland, or a diminution or arrest of some other kind of nervous action. In all of these cases, the nervous influence travels outwards from a ganglion or nerve centre towards the periphery, thus presenting an analogy to ordinary motor nerves. These facts necessitate, for practical purposes, a new physiological classification of nerves. These may be divided primarily into centrifugal and centripetal nerve fibres, and both of these may be arranged in several subdivisions. The following is a tabular view of this classification :—

NERVE FIBRES.

- CENTRIFUGAL, or conveying influences outwards from a nerve centre. Usually called *motor.*
  1. *Motor*, sometimes termed *efferent*, to muscles so as to excite contractions.
  2. *Secretory*, to the cells of glands so as to excite secretion.
  3. *Vascular*, sometimes termed *vaso-motor*, to walls of bloodvessels so as to excite contraction of vessels.
  4. *Inhibitory*, which so affect other centres of nervous activity as to moderate or destroy their action.
  5. *Connecting*, which connect motor cells in nervous centres.
- CENTRIPETAL, or conveying influences inwards towards a nerve centre. Usually called *sensory.*
  1. *Sensory*, which may cause more or less acute sensations.
     - a. *General*, convey to nerve centres in brain influences which cause sensations of a vague character, scarcely perceptible to consciousness, and not permanent.
     - b. *Special*, convey to nerve centres in brain influences which cause visual, auditory, gustatory, olfactory, or tactile sensations.
  2. *Afferent*, convey to nerve centres influences which cause no sensation, and which may or may not be followed by further nervous activity.
  3. *Connecting*, which connect sensory cells in nervous centres.

In all of these cases, the nerve fibre acts merely as a conductor, and as has been already explained, the effect depends upon the arrangements at the end of the fibre.

b. *Nerve Centres.*

All nerve centres have not the same kind of activity. When some are excited, there are sensations of pain or of light, sound, &c.; others cause movements or secretion; others are associated with psychical states; while a fourth appear to exert an influence over other nerve centres. They may be briefly classified as follows:—

(1) *Receptive Centres*, to which influences arrive which may excite sensations or some kind of activity not associated with consciousness.

(2) *Discharging Centres*, whence emanate influences which, according to structures at the other ends of the nerves connected with them, may cause movements (muscles), secretions (glands), or contractions of vessels.

(3) *Psychical Centres*, connected with sensation, in the sense of conscious perception, feeling, volition, intellectual acts, and will.

(4) *Inhibitory Centres*, which inhibit, restrain, or even arrest the action of other centres.

c. *Terminal Organs.*

It is possible that some nerve fibres may terminate in loops towards the periphery of the body or interior of organs, but it is highly probable that there is some kind of *terminal apparatus*, presenting a special structure, at the terminations of motor, and the commencement of sensory nerves. Such terminal organs are seen in the end-plates of muscle, and the rods and cones of the retina. It would appear that in normal circumstances a nerve always acts through, or is influenced by changes in, a terminal apparatus. Thus, it is highly probable that a motor nerve can excite a muscle only by the activity of the end-plates, so that when these are affected by such a poison as curare, no contraction follows stimulation of the nerve. Again, it is well known that the fibres of the optic nerve are not directly susceptible of the action of light. In normal vision, they can convey influences which, when received in the cerebrum, give rise to luminous sensations only when they have been directly excited by the retina. The same is true of the other kinds of sensory nerves. Thus there must be some kind of apparatus for the reception of the first stimulus from without, and in this apparatus changes occur which in turn excite activity in the nerve connected with it; the nerve conducts to a nerve centre; and if this centre be in a brain in a state of activity, sensation or conscious perception will be the result. The terminal organs are however not to be regarded merely as arrangements for transforming some kind of outward energy into nervous activity, but rather as stores of energy which, on the application of the outer stimulus, may be liberated and transformed into nervous energy. Thus light acting on the retina is not directly transformed into nervous energy, but it excites changes in the retina which in turn produce activity of the optic nerve.

d. *Reflex Actions.*

Impressions made on sensory nerves are conveyed to nerve centres where they may or may not be the objects of consciousness. If there be distinct perception of the impression, we have what is strictly speaking a *sensation*, which may be defined as the "consciousness of an impression." Regarding the changes occurring in a nerve centre which result in a sensation we know nothing, but it may be remarked that sensations are experienced of various degrees of intensity from the most vivid to the most vague and ill-defined. Hence it is possible that the changes which occur in a nerve centre resulting in consciousness and those causing some kind of motor phenomenon, without consciousness, may be the same in kind and only differing in degree, and that thus there may be no gap, as is usually supposed, between the two kinds of nervous activity. Motor phenomena may follow, in the living body, direct physical stimulation of the motor nerve of muscles; but this kind of action is not common. Usually motor nerves are acted upon by the will, or by emotional states, which operate upon them probably by the intervention of other nerve centres. But it not unfrequently happens that physical stimuli occasion motions in an indirect manner; the impressions being carried along sensory nerves to a central organ, where changes are excited which result in a discharge of nervous energy along motor nerves to various muscles. Thus a frog, in which the brain and medulla oblongata have been destroyed, will draw up its limbs if the foot be pinched. Such motions, unassociated with consciousness, were known to Whytt in 1754, but were attributed by him to a kind of sensation remaining in connection with the spinal cord, an opinion which has been revived in later years and has been accepted by some, but which is contradicted in the only manner possible, namely, by the facts of the clinical experience of diseases and injuries of the spinal cord of man. In 1784, the nature of actions of this kind was clearly stated by Prochaska, who also indicated in not a few instances the sensory and motor nerves which appeared to him to be the channels through which the influence causing them was conveyed, and in 1832, Marshall Hall gave them the name of *reflex actions*, and stated the conditions of this class of nervous actions in precise terms.

Reflex actions may terminate either in movement of a muscle or in secretion of a gland. A reflex movement, of the most simple type, may be thus described: (1) excitation of a *sensory* or *afferent nerve;* (2) excitation of an intermediate *nervous* or *reflex centre;* and (3) excitation of a *motor* or *efferent nerve* which causes a muscular contraction. The diagram in Fig. 38 shows this simple mechanism. It is rare, however, to find the arrangements so simple, and the mechanism may become more complex either by the existence of a number of cells or groups of cells in the nerve centre, or by the existence of numerous afferent and efferent nerves. Thus there may be such a double reflex arc as is seen in Fig. 39.

Fig. 38.—Simple reflex action. (1) sensory surface, (2) muscle; *a*, sensory nerve; *b*, nerve cell; *c*, motor nerve. The arrows indicate the direction in which the influence travels.

Fig. 39.—Double reflex action. Same description as in Fig. 38.

The three phases of a reflex action have the following general characters:—

1. The initial excitation may occur both in nerves of general sensibility and in those of the special senses; but certain nerves more easily excite reflex actions than others.

2. A reflex movement may occur whether we excite a sensory nerve at its commencement or at some point in its

course, but in the latter case the action is less intense than in the first.

3. Grey matter containing nerve cells constitutes the chief portion of reflex centres, and groups of such reflex centres are frequently associated together by internuncial fibres. The excitability is increased when these centres are severed from communication with psychical centres which preside over voluntary movements. Thus, after decapitation, reflex movements occur with greater intensity than in the uninjured animal; they are also more active during sleep.

4. Certain substances, and in particular strychnine, increase reflex excitability, so that the slightest external stimulation of the sensory nerves of the skin is sufficient to cause severe convulsions. On the other hand, bromide of potassium, hydrate of chloral, and atropine diminish reflex excitability.

5. Reflex movement may occur in one muscle, or in many muscles or groups of muscles. Thus they may be simple or compound, and when compound there may be contractions of muscles occurring simultaneously or successively. Pflüger has carefully examined and analysed the instances in which a simple reflex movement may originate a complicated series of movements, and he has formulated the four following laws, which will be understood with the aid of the diagram in Fig. 40.

a. *Law of Unilateral Action.*—If in a decapitated frog, we excite the skin of the hind foot, *p*, the excitation is transmitted from the centre *a* to the muscles (1) of the foot on the same side.

b. *Law of Symmetrical Action.*—If the excitation be more intense, it is transmitted to a centre on the opposite side *b*, and contractions may occur in the muscles of the hind limbs on both sides (1, 2).

c. *Law of Irradiation.*—If the excitation be still increased in intensity, it affects higher centres *c d*, and there may be contractions of the fore limbs (3, 4).

d. *Law of General Action.*—If the excitation be still further increased, it may pass to a still higher reflex centre *e*, and the result is general convulsions.

6. Reflex centres may be so arranged in the body as to constitute a series in which those in the cerebrum govern or control others in the deeper ganglia of the brain, while these in turn have an influence over still lower centres in the spinal cord. This arrangement has been termed the *superposition of reflexes*, and will be readily understood by studying Fig. 41.

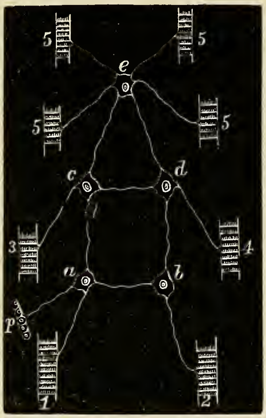


FIG. 40.—Diagram showing the relations of reflex actions. *p*, sensory surface; *a b c d e*, nerve cells; 1 2 3 4 5 5 5 5, muscles.

7. It is possible for the same stimulus to produce a reflex action of movement, a reflex action of secretion, and also a conscious perception. Thus, a stimulus, such as a strong condiment, applied to the mucous membrane of the mouth, may cause involuntary twitchings of the muscles, secretion

from the salivary glands, and a special sensation. The mechanism necessary for such manifestations is expressed in the simplest form in Fig. 42.

8. Stirling has shown that to excite a reflex action, at least one of long continuance, the stimulus requires to be repeatedly applied. There appears to be a kind of cumulative process by which the effects of stimuli reach a maximum; and when this occurs, a reflex action is the result.

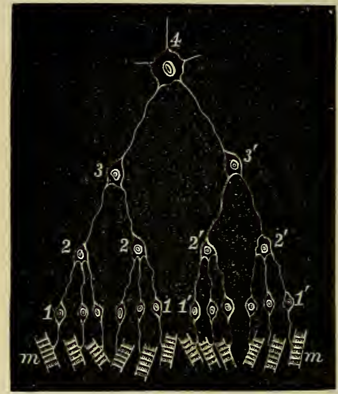


Fig. 41.—Diagram illustrating the superposition of reflexes. *m—m*, muscles; 1—1, series of reflex centres on one side, under the control of 2—2, which are again governed by 3. There is a corresponding series, 1′—1′, 2′—2′, 3′, on the other side. Both sides are presided over by 4. Thus a stimulus reaching 4 might excite the activity of all the muscles, *m—m;* if it reached 3, only one half of the muscles; if it reached 2, to the left, only three of the muscles; and finally, if it affected 1, to the left, only one muscle, *m*. (*Beaunis.*)

9. In compound reflex actions, the initial excitation may occur in psychical centres; as when the recollection of an odour causes nausea, or when a feeling of ennui is followed by yawning.

10. Some reflex movements are the result of inherited peculiarities of structure, as those made by a new-born child

when it seizes the breast, while others are acquired during life. The latter are at first voluntary, but afterwards become automatic by repetition.

The following is an enumeration of the more remarkable reflex motions, occurring either naturally or in some morbid conditions of the system:—(1) Motions of the muscles in any part of the limbs or trunk of the body under the influence of sensory impressions of the skin, such as tickling, pricking, &c.; shuddering from cold; from grating noises, &c. (2) Contraction of the pupil of the iris under the influence of light on the optic nerve. (3) Winking, or sudden closure of the eyelids from irritation of the sensory nerves of the conjunctiva. (4) Sneezing from irritation of the Schneiderian membrane, or by a glaring light in the eye. (5) Closure of the glottis and coughing from irritation of the larynx or windpipe. (6) Laughing from tickling of the skin, &c. (7) The first respiration of the child at birth from the impression of cold upon the nerves of the chest. (8) Respiratory movements in the adult

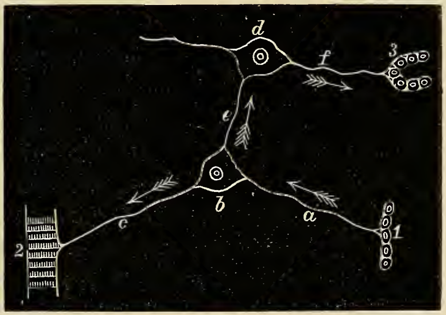


FIG. 42.—Diagram illustrating a complex reflex mechanism. The arrows indicate the direction of the currents. 1, sensory surface; 2, muscle; 3, gland; *a*, sensory nerve; *b*, reflex centre, connected with another reflex centre, *d*, by internuncial fibre, *e*; *c*, motor or efferent nerve; *f*, secretory nerve passing to gland 3. From the other side of *d* is seen a fibre passing to the brain, and there exciting changes which result in a sensation.

from the impression caused by the afferent nerves of the lungs (sympathetic or vagus), by the presence of carbonic acid in the air-cells and passages, or in those of the general system, by venous blood in the sanguiferous vessels; occasional modifications of the respiratory movements from impressions of cold, &c., on the surface of the body. (9) Suction in the infant from impression on the lips; and deglutition in the child or adult, under the influence of the impression caused by the contact of food, &c., with the fauces, pharynx, and gullet. (10) Vomiting following upon the feeling of nausea or upon the impression caused by the tickling of the palate or fauces. (11) Forced contraction of the sphincter muscles of the anus, urinary bladder, and vagina, under the influence of local irritation. (12) Erection and emission under the influence of irritation of the nerves of the penis and other parts in the vicinity. (13) Rhythmic action of the lymphatic hearts (in the frog), under the influence of the upper and lower parts of the spinal cord, and perhaps of the presence of fluids within the cavities of the lymphatic hearts. (14) Rhythmic action of the sanguiferous heart, under the influence of the cardiac ganglia, and the impressions produced by the presence of blood in the cavities. (15) Peristaltic motions of the stomach and alimentary canal, in digestion and in the process of defecation, &c., under the influence of impressions conveyed to the ganglia by the various splanchnic and intestinal nerves. (16) Expulsive action of the urinary bladder under the presence of urine. (17) The expulsion of the child from the uterus in parturition, under the influence of the hypogastric and other ganglia, and of impressions conveyed to them. (18) Contractions and dilatations of the bloodvessels and secreting ducts, under the influence of the various sympathetic and cerebro-spinal nerves distributed to them; blushing, flow of tears, bile, &c.

In the first of these examples, the reflexion of the influence, or its reflex excitement, may occur through any part of the cerebro-spinal centre; in the second, through the thalami optici and corpora quadrigemina; in the third and following examples to the tenth, the medulla oblongata is the principal centre of reflexion; in some of these, and in the eleventh, twelfth, and thirteenth, various parts of the spinal cord; and in the remaining examples, the various ganglia of the sympathetic system appear to be the principal centres of reflexion; but yet subject, in a remarkable manner, to modification from the action of some parts of the cerebro-spinal centres, as will be more particularly stated in treating of the spinal cord and brain.

Reflex stimulation of the voluntary muscles takes place chiefly through the cerebro-spinal centres; that of the involuntary muscles principally through the sympathetic ganglia; but it would appear that occasionally reflex actions may be excited in either of these kinds of muscles, through those parts of the nervous system which constitute respectively the more usual centre of action of the other. Many obscure and probably complex actions may be of this kind, as, for example, some of the motor and sensory affections produced by intoxication, the nervous impression acting primarily on the stomach; palpitations of the heart, or cramps in the limbs, from stomachal and intestinal derangements; fainting from concussion, from peculiar odours, or from mental affections; dilatation of the pupil, and grinding of the teeth from the irritation of worms; various other affections from teething, &c. (*Allen Thomson.*)

Consult WHYTT on the Vital and Involuntary Motions, 1754; PROCHASKA, De Funct. System. Nervos., Prague, 1784, and Opera Minora, 1800; MARSHALL HALL, first papers in Trans. Zool. and Royal Soc., 1832 and 1833, and Memoirs on the Nervous System, 1837, and other works; MÜLLER'S Physiology by Baly, vol. I, p. 754; PFLÜGER, Die Sensorischen Functionen d. Rückenmarks, Berlin, 1853; SETSCHENOW, Ueber die Hemmungsmechanismen für die Reflexthätigkeit des Rückenmarks, Berlin, 1863. See also two interesting papers by STIRLING in the Edin. Med. Jour., 1877, and an article by WUNDT in "Mind," 1876.

VII.—PHENOMENA OF FILTRATION AND OF ENDOSMOSE IN RELATION TO TISSUES.[1]

The general properties of the various tissues have been already described; but there are several of a physical character which play so important a part in nutrition as to merit special attention. These are the physical processes of filtration and of endosmosis through organized membranes.

1. FILTRATION THROUGH ORGANIC MEMBRANES.

When we pour a fluid into a glass cylinder, one end of which is covered by an organic membrane, if the membrane imbibe the fluid, or a portion of it, filtration occurs. The rapidity of filtration is in direct relation with the pressure exerted by the fluid upon the membrane, and it increases very rapidly with a rise of temperature. Solutions of crystalloids pass almost without change, and the density of the fluid left behind is the same as that which has passed through the membrane. In the case of colloids, however, the proportion of the dissolved substance is always less in the filtered fluid than in that which remains behind; or, in other words, a membrane permits the passage of a larger relative quantity of water than colloids.

When colloids exist in a fluid, they exert an influence upon the filtration of the salts dissolved in the same fluid; the proportion of salts which passes through is always greater in relation to the salts left behind, as the quantity of

---

[1] The following has been chiefly prepared from Wundt's elaborate account in his Physiologie Humaine, p. 55.

colloidal matter is smaller in the filtered fluid; or, in other words, the presence of colloidal matter hinders the filtration of crystalloids. The filtration of fluids flowing in vessels is affected in the same manner by pressure and temperature; but certain phenomena which occur can only be explained by assuming special properties in some organic membranes.

2. DIFFUSION THROUGH ORGANIC MEMBRANES.

When an organised membrane is interposed between two fluids, both of which may be imbibed by the membrane, and may mix together, an exchange of the two fluids takes place through the membrane, and this exchange goes on until the two fluids have the same composition. There may be, however, an unequal exchange between the two fluids, so that for one part of the first fluid which passes to the second, a smaller quantity will pass from the second to the first. Temperature has an influence on diffusion. In comparing the diffusive properties of different fluids, it is necessary to make the experiment at the same temperature, and with one of the fluids constant in composition. Distilled water is therefore employed, in comparative experiments, as the standard fluid. Suppose a saline solution is placed in a glass tube, closed at the bottom by an organic membrane, and the apparatus is immersed in a shallow vessel nearly filled with water, some of the salt will be found after a time to have passed into the water, and some of the water will have passed through the membrane into the tube. It will also be found that there is a constant relation between the weight of the water which has passed in the one direction, and the weight of the salt which has passed in the other. The quantity of water which passes is always a multiple, or, in some cases, a fraction of the quantity of the substance in solution which diffuses. The weight of the quantity of water necessary to replace by diffusion a unit of weight of the dissolved body, is called the *endosmotic equivalent* of the body. This equivalent depends (1) on the chemical nature of the body; and (2) on the degree of concentration of its solution. The following table, given by Jolly, shows the equivalents of certain substances:—

Name of Substance.	Endosmotic Equivalent.
Chloride of Sodium,	4·0
Sulphate of Soda,	11·0
Sulphate of Potash,	12·0
Sulphate of Magnesia,	11·5
Sulphate of Copper,	9·5
Sulphuric Acid,	0·3
Caustic Potash,	200·0
Alcohol,	4·3
Sugar,	7·2

As Jolly, in these experiments, took no account of the degree of concentration of the fluids, and as he always employed dried membranes, these figures do not show the quantities of these substances which would pass through organic membranes in the living state. Hoffmann has shown also that the amount of water of hydration or of crystallization, even in the same salt, influences, to a remarkable extent, the endosmotic equivalent.

When more water passes towards the saline solution than the amount of the latter which enters the water, the diffusion is said to be *positive*, and *negative* when the reverse is the case. With alkalies positive endosmosis is strong; with acids, negative endosmosis is the rule, while salts are positive and range between the two extremes. When endosmosis is positive, the equivalent increases with the degree of concentration; when, on the contrary, it is negative, the equivalent diminishes as the concentration increases. Thus, in the diffusion of sulphuric acid with water, more acid will pass into the water as the acid becomes concentrated; but, on the contrary, in the diffusion of potash with water, more water will pass into the potash as the latter is concentrated. According to Ludwig, sulphate of soda is an exception amongst bodies showing a positive endosmosis, as its equivalent diminishes by concentration.

Diffusion occurs with a *constant rapidity* so long as the solution has the same concentration, and as the temperature remains the same. This rapidity, however, does not depend only upon the endosmotic equivalent, but also upon the solubility of the substance and its chemical composition. It increases with concentration. When saline solutions diffuse into water, the rapidity with which the salt passes towards the water, as well as that with which the water passes to the salt, increases with the degree of concentration, but not at the same rate. The rapidity with which the water passes to the salt becomes greater, whilst the rapidity with which the salt passes to the water remains nearly proportional to the degree of concentration. Thus it follows that the more a solution approaches saturation, the greater is the quantity of water which passes in the same time. As the temperature increases, the rapidity of the diffusion also increases, and the rapidity of diffusion increases more rapidly as the temperature rises. This will be seen in the following table, given by Eckhard, showing the rapidity with which common salt passed through the fresh pericardium of an ox in the same time with an increasing temperature:—

Temperature in Degrees C.	Quantity of Common Salt which passed.
8·0,	0·303
9·6,	0·364
13·8,	0·396
18·3,	0·474
22·5,	0·549
26·0,	0·628

When a solution diffuses through a membrane not only with water, but with a solution of the same or of a different substance, that is, where two solutions of the same substance or of different substances, are on opposite sides of the membrane, the diffusion depends partly on the degree of concentration of the two solutions, and partly upon the chemical properties of the two bodies dissolved. Suppose two solutions of the same substance, but of unequal degrees of concentration; the more concentrated solution will diminish, while the more dilute will increase in density. In this case, the endosmotic equivalent has a constant value. On the other hand, the rapidity of diffusion will be in the inverse ratio of the difference of concentration of the two fluids present; that is to say, as the initial difference of concentration of the two fluids diminishes, the rapidity of diffusion will also become slower.

All colloidal substances in solution pass with great difficulty through organized membranes. Such bodies attract water, so that, when their solution diffuses with this fluid, there is a reverse current of water. The endosmotic equivalent of these substances is very high, but on the other hand the rapidity of their diffusion is low. Albumen in solution has a stronger endosmotic affinity for saline solutions than for water, and the current of albumen increases very rapidly with concentration of the saline solution. When a mixture of colloidal bodies in a fluid along with some crystalloids, is permitted to diffuse into water, none of the colloidal matters pass through the membrane. Thus from a solution of gum, albumen, and sugar, none of the first two will pass, but the sugar will pass through with great ease. There is thus a kind of mechanical separation of the substances. To this general rule, however, there is one exception, namely, when by the diffusion of a substance mixed with colloidal matters, there is produced on the other side of the membrane a liquid toward which the colloidal matter has a great tendency to diffuse. Thus when a mixture of albumen with common salt is exposed to diffusion into water, the salt alone at first passes through the membrane, but when the water on the other side of the membrane contains a certain amount of salt, the albumen then diffuses with considerable intensity. Von Wittich and Funke have studied, as regards diffusion, the differences of solutions of various albuminoids, and they have found that of these bodies, peptones possess the property of diffusibility to the greatest extent.

A continuous electric current passed through a fluid, in a diffusion apparatus, affects diffusion; the quantity of fluid situated on the side of the negative pole increases, whilst that on the side of the positive pole diminishes. The mass of fluid moves in the direction of the positive current, and the quantity of fluid carried away is always greater as the fluid is easy to move and as the galvanic current is more intense, and the amount is independent of the nature of the surface and of the thickness of the porous plate. (*Wundt.*)

When water is allowed to diffuse with a saline solution, and a galvanic current is directed through the two liquids from the water to the salt, more water will pass to the saline solution than would have passed if the current had not been there. If now the direction of the current be changed, so as to pass from the salt to the water, more salt will then pass towards the water, or, in other words, the endosmotic action has been inverted by the galvanic current.

Albumen is found in the body combined with alkalies, as albuminate of soda or of potash, behaving in these compounds as a feeble acid. Suppose that albumen and saline matters are submitted to diffusion with water, and that at the same time a current is passed through the solutions, it will be found (1) if the positive current be directed from the solution of albumen towards the water, salts will pass from the side of the water, and albumen will remain near the positive pole; (2) if the current pass from the water to the albuminous solution, water will pass to the albuminous solution, and albumen will pass through the membrane into the water, and will be deposited near the positive pole. The albumen then behaves as acids do, having passed from the negative towards the positive pole. These interesting facts, ascertained by Von Wittich, indicate the possibility of the physical phenomena of nutrition being affected by a continuous galvanic current, and they suggest many researches of therapeutical importance. (*Wundt.*)

The nature of the membrane affects endosmotic action. Dry membranes have always a higher endosmotic equivalent than those which are fresh or wet. In comparing organic membranes of different structure, it is found that the dimensions of their pores have an important influence, just as is known to be the case in diffusion through plates of clay. Buchheim has shown that for a membrane with large pores, the endosmotic equivalent of a salt is smaller as the affinity of this salt for water is greater, while, on the other hand, for very dense membranes, the equivalents are proportional to the affinity of the salts for water. The following table by Harzer shows the variations of endosmotic equivalents for different membranes.

	Ox Bladder.	Pig's Bladder.	Ox Pericardium.	Collodion Membrane.
Chloride of Sodium,	6·460	4·335	4·000	10·200
Chloride of Potassium,	5·601	——	3·891	13·632
Sulphate of Soda,	18·764	12·231	8·915	6·097
Sulphate of Potash,	13·908	11·700	8·181	4·147

Of all of these membranes, that formed of collodion is the most dense; the bladders of the ox and the pig are both less, and the pericardium of the ox occupies a mean position. The sulphates have a much stronger affinity for water than the alkaline chlorides.

All the phenomena of endosmose may be attributed to the following causes: (1) to a force of attraction of two fluids, the one for the other; (2) to a relative attraction that the substance forming the membrane exercises upon the two liquids in diffusion,—a force which determines the mode in which liquids pass, and the rapidity with which they pass, through small porous canals; (3) to the narrowness of the pores through which the liquids pass; and (4) to the diminution of adhesion of the liquid to the wall of the porous canals, by reason of elevation of temperature. Brücke was the first to attribute the phenomena of diffusion to an attraction between the walls of canals and water.

The importance of applying these facts regarding filtration and endosmose to the phenomena of the nutrition of living tissues is becoming more and more recognised. In the present state of our knowledge, however, it is impossible to follow all the stages of the process, and we can only make general statements.

The connective tissues are surrounded on all sides by fluids such as blood, serous transudations, and lymph. These fluids may be regarded as saline solutions of albuminous matters, or as solutions containing both crystalloids and colloids. The fluids are imbibed by the connective tissues just as they would be taken up by porous substances, by a process which may be called *capillary imbibition.* But when the fluids reach the ultimate tissues in the form of protoplasmic masses, or of protoplasm more or less modified, we have to deal with a homogeneous structure containing no pores. Here an interchange occurs between the fluid and the tissues by a kind of *molecular imbibition,* a process similar somewhat to that by which a membrane, as above stated, allows osmotic phenomena to occur. Molecular imbibition possesses the two following characters: (1) When a tissue imbibes a fluid, it usually increases in volume, but this increase does not always correspond to the quantity of the fluid imbibed, and in some cases actual diminution in size of the mass of tissue may occur after imbibition; and (2) tissues imbibe more distilled water than water containing saline substances, and consequently the fluid which is imbibed by a membrane will be less concentrated than the fluid in which the membrane is immersed. This probably explains why serous effusions are in general less concentrated than the plasma of the blood. (*Beaunis.*)

The passage into the tissues of part of the plasma of the blood through the thin walls of the capillaries, under the influence of blood pressure, is an example of filtration. The greater the amount of pressure exerted in the vessels, the greater will be the amount of fluid forced through their walls. A similar phenomenon is seen in the separation of water and saline matters from the blood in the Malpighian bodies of the kidney, where the blood passes under considerable pressure through a complicated arrangement of minute vessels. Colloidal matters, such as albumen, in these circumstances pass with difficulty, and only under strong pressure, whereas, on the other hand, crystalloids pass more readily, and under feeble pressure. Any circumstances, therefore, which increase beyond a certain limit the pressure in the vessels may be attended by the appearance of albumen in the urine.

It is to be especially noted that in the living body we rarely find the conditions of endosmotic phenomena so simple as to consist of a fluid on each side of a membrane, and each under the same pressure. Almost invariably one of the fluids is under a greater pressure than the other, and thus the interchange that takes place must be due partly to filtration and partly to endosmotic action. In addition it is possible that there may be some kind of attractive influence exerted by the living tissues themselves, and thus the process by which they obtain fluid pabulum becomes more complicated. A special influence of this kind, to be remembered in studying secretion, by which certain matters are removed from the blood, is the *selective activity* of epithelial cells, of which examples will be given in treating of secretion.

3. Diffusion between Gases and Fluids through Organized Membranes.

Diffusion between gases and liquids is not modified in its essential points by the interposition of a wet organic membrane. The gas is absorbed by the membrane and passes into the fluid. When the fluid contains at the same time a gas, a portion of it is eliminated and is replaced by an equivalent of the external gas. The *coefficient* of *absorption* of a gas is the volume dissolved by one volume of water at 0° C and 760 mm. pressure. The quantity of gas exchanged between two gases on opposite sides of a membrane, one of them being dissolved in a fluid, depends partly on the coefficient of absorption of the gas and partly on the pressure of the gases on opposite sides of the membrane. The gas which possesses a large coefficient of absorption, as carbonic acid, is absorbed by a wet membrane in greater quantity than oxygen, hydrogen, or nitrogen. The capacity of absorption diminishes with the elevation of temperature and with a diminution of pressure. Absorption, in addition to the specific attraction which a liquid may have for a gas, depends upon the quantity of the external gas; the greater this quantity, the greater is the pressure and the greater is the amount of gas absorbed by the fluid. When a state of equilibrium between the tension of the gas in the fluid and that of the external gas is attained, absorption ceases. If the pressure of the external gas diminishes, and that of the internal gas increases, there will be a current in the outward direction, so that the gas dissolved in the fluid will pass into the external gas until a state of equilibrium of pressure is re-established. There is thus a state of continual gaseous exchange established between fluids of the body in which gases are dissolved and the external atmosphere. This process, as we shall hereafter see, is the essential phenomenon in respiration, as it occurs in the ultimate air cells of the lung. It is highly probable that the same physical explanation may be given of the interchange of gases which constantly occurs between the gases dissolved in the blood and those set free in living tissues, as one of the ultimate chemical products which are the result of their vital activity.

Consult, regarding the laws of absorption and of diffusion of gases, Wundt's Physique Médicale, p. 201.

VIII.—VITAL PHENOMENA OF THE TISSUES.

By vital phenomena we mean those which occur in living textures, or in living organisms, and which at present cannot be satisfactorily explained by the application of physical or chemical laws. Most of these phenomena have been already described in treating of the various tissues, and others will be alluded to in the description of the functions of nutrition, innervation, and of reproduction. It will be useful, at this stage, to enumerate them as follows: (1) irritability and contractility of muscle; (2) excitability of nerves; (3) movements of protoplasm, either in the free state or included in cells; (4) movements of cilia; (5) the functions of assimilation and of disassimilation occurring in the living cell; (6) the multiplication of the cell, either by endogenous formation, by segmentation, or by budding; (7) the production of one or both of the elements necessary for the production of offspring; and (8) the changes occurring in the brain which are associated with mental acts.

IX.—APPLICATION OF THE LAW OF CONSTANCY OF ENERGY TO VITAL PHENOMENA.[1]

In order to understand the application to living organisms of the views now held by natural philosophers regarding energy and force, it is necessary in the first place to state several general principles.

In every chemical combination the elements are held together with a certain force, and this force may be measured by the resistance which these elements oppose to separation. Elements which are already in combination have only a feeble tendency to unite with the elements of other combinations. But if from external causes the combination of elements be broken up, each individual element will then show a strong tendency to enter into a new combination. Thus the oxygen in carbonic acid manifests only a feeble tendency to enter into combination with a body oxidisable by free oxygen. Again, when one or more elements in a body are in a state of loose combination, these elements are more ready to unite with some other substance. The forces which are thus limited to a simple tendency to movement may be termed forces of tension, or energy in a potential state, or simply *potential energy;* those, on the other hand, which exhibit actual movement may be called actual forces, or *actual*

---

[1] The following account is obtained from WUNDT'S Physiologie Humaine, p. 108, *et seq.*

energy. Sometimes, also, actual forces are termed *kinetic*, whilst potential forces receive the name of *kinematic* energy.

The tendency which a chemical element possesses of entering into combination is a force of tension, the intensity of which is variable according as the element is free or combined, or in a combination more or less stable. An element which shows an increased tendency to combination has its chemical force of tension increased; a free element which enters into a combination has lost its tendency to combine, and its force of chemical tension is thus diminished. Every chemical decomposition gives rise to a force of tension, and in every chemical combination a force of tension is apparently lost. When elements pass from a stable combination to one less stable, a force of tension is developed; and when they pass from a less stable to a more stable combination, a force of tension disappears. It follows, then, that in every chemical combination actual forces are developed, and in every chemical decomposition actual forces disappear. The sum of all actual and potential forces is always constant. That which is lost as an actual force is transformed into a potential force, and that which is lost as a potential force is transformed into an actual force. In all the phenomena of nature it may be shown that in every transformation there is a conversion of actual into potential force, or the reverse.

The law which states that the sum of the actual and potential forces is always constant is called the law of the *constancy of force.* The different forms of actual energy with which we are acquainted are the movements of bodies, light, heat, and electricity. All of these forms of actual energy show a tendency to be transformed into one, namely, heat. When movement disappears by friction, or by the resistance of the air, it is transformed into heat; when electricity encounters resistance in its progress, it is also transformed into heat. The form of movement which appears as actual energy in chemical combinations is principally heat, less frequently light, and the same also which disappears in chemical decompositions is heat and light.

The distinction between actual and potential energy will be better understood by studying the phenomena of a falling weight. A weight suspended by a cord represents a certain force of tension, a tendency to fall, measured by the tension which it exerts upon the cord. If the cord be cut, the weight falls, and the force of tension becomes an actual force, which may be measured by the mechanical effect produced by the weight upon the ground. All the tensional force possessed by the weight has now been transformed into actual force. If the weight be again raised, as by turning the cord round an axle, the tensional force will be again restored, at the expense of an amount of actual force used in the muscular contractions of the arm winding up the cord, which will be equal to that developed by the weight during its fall. The fall of the weight transformed potential into actual energy; when it was raised, actual energy was again re-transformed into potential energy.

The general principles above stated may now be applied to the phenomena of plant and animal life. When a plant assimilates the inorganic compounds from the atmosphere which are necessary to its nutrition, it does so in virtue of a power which exists in the germ, and which belongs, more or less, to the histological elements of the plant derived from this germ. This force of affinity takes its origin from the chemical combinations which constitute the elementary parts of the plant, and it differs according to the nature of these elements. Thus the green leaves attract carbonic acid from the atmosphere, and the roots carbonic acid in solution, ammonia, and mineral matters. These forces of chemical affinity depend on fixed external conditions. It is under the influence of the sun that the trees develop buds and leaves, and it is equally under the influence of light that green leaves absorb the carbonic acid necessary for vegetable life. Under the influence of light and heat, the elements carbon, nitrogen, hydrogen, and oxygen, obtained from carbonic acid, water, and ammonia, enter into combinations more unstable, such as the albuminoids, fats, and carbo-hydrates, whilst at the same time the greater part of the oxygen is set free. According to the law of the constancy of energy, a part of the actual energy coming from without is transformed into potential energy, and the actual energy which has disappeared is the actual energy of solar heat and light. Whilst a plant is nourished, the actual energy of solar light and heat is transformed into potential energy in the chemical elements forming the plant. The plant is then an organism which transforms actual into potential energy. The animal consumes the substances formed by the plant, and thus introduces into its body a large amount of potential energy. These substances are decomposed in the body of the animal by a constant oxidation, and this oxidation sets at liberty the forces of affinity which were in a state of repose in the assimilated substances. The forces thus set free manifest themselves in the animal body partly in the form of heat, partly in muscular movements, and partly in nervous action. An animal is then an organism which transforms potential into actual energy; a process the reverse of that of the plant. The plant furnishes the animal with the quantity of potential energy necessary for being transformed into actual energy; but the actual energy developed by the animal is not directly re-transformed into the potential energy of the plant. The plant is therefore always receiving new supplies of potential energy from the solar rays. Thus the forces of organised beings depend ultimately upon solar heat and light. The plant receives these forces directly from the solar rays; the animal, on the other hand, receives them only indirectly through the intervention of the plant.

As already stated, the actual energy of the living body appears under the form of heat and the mechanical work of muscles. If the body be analogous to machines in which, by chemical actions, heat and movement are developed, it follows that it is the oxidation of assimilated substances by the oxygen inspired which produces the heat and movement of the body. Applying the law of the constancy of energy, it is evident that, supposing the amount of combustible matter to be constant, the heat set at liberty may be compensated by an equal amount of mechanical work; or, inversely, that the mechanical work developed may be compensated by a loss of an equivalent amount of heat. In other words, the quantity of potential energy transformed into actual energy—heat—cannot at the same time be transformed into actual energy in the form of mechanical work. The application of the views above stated will receive illustration in treating of animal heat.

X.—THEORIES OF LIFE.

Numerous efforts have been made to define life, of which the following are examples: *Aristotle* says "Life is the assemblage of operations of nutrition, growth, and of destruction;" *Lamarck* states that "Life, in the parts of the body possessing it, is that state which permits organic movements, and the movements which constitute active life result from the application of a stimulus;" *Bichat* says, "Life is the sum total of the functions which resist death;" *Treviranus* calls it "the constant uniformity of phenomena, with diversity of external influences;" *Laurence* says it consists "in the assemblage of all the functions or purposes of organized bodies, and in the general result of their exercise;" *Duges* calls it "the special activity of organized bodies;" *Béclard's* definition is "organization in action;" and *Herbert Spencer* asserts that "life is the continual adaptation of internal relations with external relations." It will be observed from the above definitions that authors have felt the necessity of presupposing some organized structure, the existence of which is taken for granted in their definitions. The dictum of Béclard, "organization in action," is, on the whole, the best.

Various theories have from time to time been offered by philosophers to explain the existence of life, either as a special phenomenon of matter, or as a conscious condition. Some have supposed that life was an independent principle, capable of being added to or removed from matter. Others have thought that the phenomena of life resulted from the action of an immaterial and conscious existence or principle, *the soul*, acting directly or indirectly on the mechanism of the body. A third class of thinkers have imagined that vital actions come under the same laws as physical actions, and that vital acts are directly affected by external conditions. From the point of view of the physiologist, who has to deal with direct observation of normal phenomena, or phenomena as modified by experiment, it is not necessary to assume the operation of a living principle independent of matter, (as we are acquainted with matter and its varied activities by methods of research employed in the present day,) although, upon evidence of an entirely different kind, he may be convinced of the existence of such a principle. It is not within the province of this work to discuss theoretical views regarding the question, and it is sufficient to point out that it is the duty of the physiologist to investigate the *conditions* in which vital phenomena occur, and that he ought not to be expected either to furnish definitions of life or to offer an explanation of the correlation which undoubtedly exists between mental phenomena and the physico-chemical changes known to occur in the brain. Such definitions and such explanations are of no value, inasmuch as, in the present state of science, our knowledge of vital processes is deficient, and as it is probable that the molecular changes which we associate with vital phenomena may never be thoroughly understood. What is termed *vital* may simply be a condition of matter; but even if it were found to be so, it would be none the less mysterious. The intimate nature of the phenomena of gravity, chemical activity, magnetism, and electricity, is just as obscure as that of vital actions. Or, to put the statement in another form, the growth of a cell, the contraction of a protoplasmic element, or the connection between a change in a portion of grey cerebral matter with a sensation or an emotion, are processes no more inexplicable than the influence of a current of electricity on a magnetic needle, or the falling of a stone to the earth.

Having now described the chief chemical, physical, and vital properties of the tissues, or what may be termed GENERAL PHYSIOLOGY, we next pass on to the consideration of the physiology of the individual. This includes a description of the functions of the various organs and systems found in the body, or SPECIAL PHYSIOLOGY.

SPECIAL PHYSIOLOGY.

The special functions of the human body may be considered under the heads of nutrition, or the exchange of materials, innervation, animal movements, production of heat and maintenance of a uniform temperature, and reproduction.

NUTRITION.

Nature of Nutrition—Stages of Nutrition—Alimentary Substances and Digestion—Absorption—Sanguification—The Blood—Circulation of the Blood—Respiration—Nutritive Changes in the Tissues—Secretion—Elimination—Excretion.

By nutrition is understood a series of functions by which matter is introduced into the body, becomes for a time incorporated with the tissues and fluids, and is afterwards separated from the body by various channels. As a result of this exchange of material between the organism and the external world, the various functions of life are performed. At one time, the term nutrition was strictly limited to the process by which the living tissues took up from the blood matters necessary either for their repair or for the due performance of healthy functions; but it is more convenient for practical purposes to regard nutrition as really a complex process, involving a number of subsidiary processes, all of which have for their object the maintenance in healthy action of every tissue and organ, and of the body as a whole. This mode of regarding nutrition will be found useful to the student of medicine when he is called upon to study the phenomena of disease. Thus in the great majority of diseases, the emaciated look and the feeble movements of the patient indicate that the process of nutrition is somehow or other not duly performed, and it becomes the duty of the physician to ascertain what stage or stages of the process are interfered with. In some cases it will be found that the error lies in the processes by which food is prepared for assimilation, in other cases there is failure in some of the operations by which blood is formed, in a third class the apparatus by which this blood is circulated through the body and brought into close contact with the living tissues is not working in a proper manner, whilst in many others nutrition is not duly performed in consequence of the fault of one or other of the excretory organs, by which waste matters which would exercise a baneful effect on living tissue are eliminated from the blood. The student should thus habituate himself to the observation of diseased conditions from the physiological point of view, and this habit, as has been well written by Hughes Bennett, not only leads him to see how nutrition may be deranged in so many ways, but to arrive at the scientific explanation of those complications in diseases which he is constantly meeting with. It must lead him to the conviction that impaired nutrition is to be treated by an endeavour to restore the deranged processes to their healthy state in the order in which they are deranged; that for this purpose a sound knowledge of the process of nutrition itself is a preliminary step; that empirical systems can be of little benefit, and that the only correct basis for medical interference is a comprehensive and true physiology.

The process of nutrition consists of the following stages :—

1. *Digestion*, or the chemical and physical processes by which the food is prepared in the alimentary canal for absorption. This includes the various mechanical actions by which the food is broken down in the mouth, swallowed, and propelled along the alimentary canal ; and also the physical and chemical actions of various fluids mixed with the food, such as the saliva, gastric juice, intestinal juice, pancreatic juice, and the bile.
2. *Absorption*, or the process by which fluid matters, and matters prepared by digestion, pass into channels which ultimately convey them to the blood.
3. *Sanguification*, or the preparation of a nutritive fluid called the BLOOD, which receives fresh materials from the digestive canal, oxygen from the process of respiration, and cellular elements from certain glands called blood-glands, found in various parts of the body.
4. *Circulation*, or the mechanism by which the blood is propelled through the body so as to bring it into close relation with almost every living elementary constituent.
5. *Respiration*, or the interchanges which occur between the gases of the body and the gases of the air, and consisting essentially of the introduction of oxygen and the elimination of carbonic acid. The process of respiration may be divided into two stages : *external* respiration, or the mechanism by which there is an exchange between the gases of the blood and the gases of the air in the pulmonary cells : and *internal*

respiration, or the exchange which occurs between the gases of the blood and the gases of the living tissues.

6. *Assimilation*, or *Nutrition*, the processes by which living tissues take from the blood nutritive materials which may become for a time incorporated with the protoplasm of the tissues, and thus undergo molecular changes converting them from dead into living matter. Under nutrition, it is important also to study a process, termed the *glycogenic function*, by which the liver forms glycogen, or animal starch, a substance which after conversion into sugar, is of the greatest importance in healthy nutrition. It is evident that the great object of this process is (1) to repair the waste which the living tissues undergo, more or less, as a condition of the healthy performance of their functions, and (2) to supply to the tissues matters which they may utilize, for the evolution of energy, in a manner analogous to the consumption of fuel by a machine. The process of *growth*, by which a tissue or organ may increase in size, is included also under nutrition.

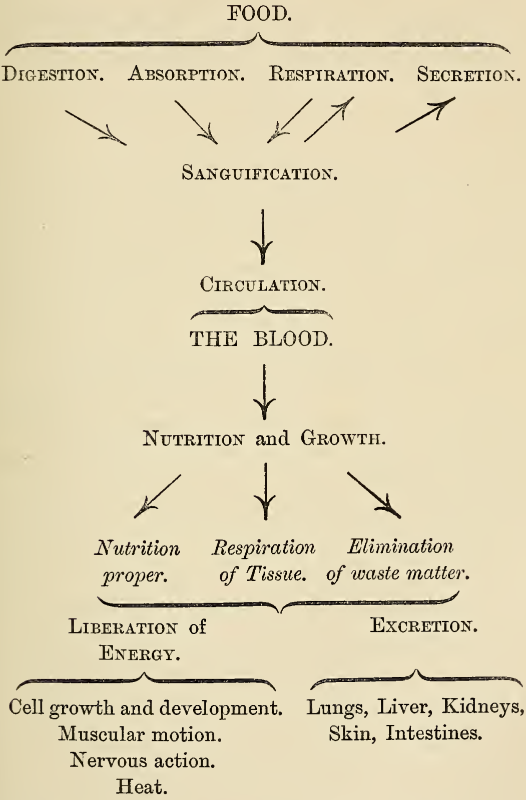
7. *Secretion*, the process by which certain matters are separated by the cells of glands from the blood, and elaborated by these cells so as to form the various secretions, such as saliva and the other digestive fluids. It will be found that the phenomena of secretion depend chiefly upon the development and growth of cells.

8. *Elimination*, and the formation of *Lymph*. As already mentioned, one of the conditions of the functional activity of tissues is the occurrence of chemical changes which lead to the formation of simpler

chemical compounds. These chemical changes may often be accompanied by a physical degradation of structure, as in the formation of fat globules in various cells. The matters thus formed, constituting what may be called the *waste products* of the mechanism, must be removed in most cases as quickly as they are formed, because their presence interferes with due performance of function. Their removal is effected partly by the capillaries, but chiefly by a separate set of channels termed the *lymphatics,* and the waste matter is conveyed by these lymphatics to certain glands in which at least a portion of it may be again prepared for nutritional purposes. In addition to these waste materials, *lymph* contains the excess of nutritious matter which has transuded from the bloodvessels, and which has not been used up by the living tissues.

9. *Excretion,* by which matters hurtful to the body are separated by various channels. The phenomena of excretion are partly mechanical, as in the evacuation of the fæces, partly depend upon the physical process of pressure forcing fluid matters through thin walled tubes, and partly upon cell-development and growth, as in secretion. Excretion is carried on by five channels,—the lungs, the liver, the kidneys, the skin, and the intestines.

The student should familiarize himself with the view that the early stages of the process of nutrition are intended for the preparation of the blood, the medium by which the tissues are nourished and in which they respire, and that the later stages have as their object the maintenance of this fluid in a state of purity. As a result of ultimate nutritional changes, energy is set free in the form of cell growth and development of tissue, muscular and nervous action, and heat. This view may be fixed upon the mind by studying the following diagram, in which the arrows represent graphically the direction of the processes with reference to the blood.



Having given this general survey of the function of nutrition, we shall now enter into details regarding its various stages.

I. DIGESTION.

The process of digestion consists of the physical and chemical transformations to which the food is submitted in the alimentary canal, so as to prepare it for absorption. Before entering upon an account of these transformations, it will be necessary to consider the general characters of food.

FOOD.

Under the name Food we include those substances, either in the solid or the fluid form, which are required for the nutrition of the body. The body is constantly undergoing various changes, both chemical and physical, which are conditions of vital activity. Chemical transformations occur, and simpler chemical compounds are formed, which may be regarded as waste products, to be removed from the body. There is thus a loss of material constantly taking place. But, as has been already seen, there is also an almost constant expenditure of energy in movement, heat, &c.

To make up for the loss of material and of energy, food must be supplied. Food may be regarded as matter in a condition favourable for the liberation of energy under the action of the influences at work in the body. Thus the supply of food meets the demand both for matter and for energy. Apart from energy, as already said, the matter of food supplies materials to make up for the loss of matter which the body sustains as a condition of its life. There is thus, in the economy, a gain on the one hand and a loss on the other. If the gain to the organism, by alimentation, be in excess of the loss, as occurs in early life, the body grows, and the amount of growth is in direct proportion to the excess of the matters entering the body over those which are removed. When the gain and the loss are about equal, as usually occurs in middle life, the weight of the body is stationary; and when, in advanced life, the loss is in excess of the gain, the body loses weight.

It has already been seen that the human body consists of water, salts, albumenoid matters, fats, and carbohydrates. The same proximate principles are required as food. It is rare, however, that food, in the common sense of articles of diet, consists of one proximate principle only. An article of diet usually consists of a mixture of one or more proximate principles. Thus, water holds various salts in solution; butcher meat contains albumenoids, fats, salts, and water; and milk, which may be regarded as a typical form of food, inasmuch as it is sufficient for the nutrition of the young of all mammalia, contains, in due proportion, all the proximate principles.

1. PROXIMATE PRINCIPLES OF FOOD.

The following are the principal points to be noted by the student with reference to the simple proximate principles.

1. *Water.*—Water, suitable as an article of diet, must be fresh, limpid, without odour, and having an agreeable taste. It ought to contain a certain percentage of gas and of mineral matters in solution, and to be completely exempt from organic matter. The agreeable taste of water depends principally on the carbonic acid and salts which it contains. This taste, or sharpness, is well marked in gaseous waters, which may be either natural or artificial. The mineral matters in good water should not exceed 30 centigrammes of residue per litre. The salts consist of carbonates, sulphates, and alkaline and earthy chlorides.

The quantity of water in the body is maintained at a uniform amount by a balance being struck between the quantity introduced and the quantity lost by exhalation from the lungs and evaporation from the skin. When the quantity falls below a certain minimum, a sensation of thirst is experienced; and, if the amount fall still lower, certain well marked physiological effects are produced which will be afterwards described. The introduction of water into the body in excessive amount is not without a certain effect upon the body, as is generally supposed. On the contrary, it increases the pressure of the blood, and consequently produces the physiological effects of increased pressure; and, in addition, there is an increase in the amount of urea, and of mineral matters, separated by the kidneys.

2. *Mineral Matters.*—Mineral substances are indispensable in the food. They are active agents in nutrition, and their presence in the fluids and solids of the body appears to be essential. When an animal is entirely deprived of mineral matters in its food, less of these substances appear in the excretions, and the animal quickly falls out of health. The most important salt is *chloride of sodium,* which is found in all the fluids, tissues, and organs of the body, and which is taken as an article of diet, instinctively, both by man and animals. About 20 grammes of common salt are separated by the various excretions in 24 hours, and the same amount must therefore be supplied in food. Most articles of diet do not contain enough of common salt, indeed, the amount is usually insignificant, and, consequently, most of it is taken directly, either as a condiment, or in salted food. It has been shown that when an animal receives chloride of potassium instead of chloride of sodium in its food, after a certain time the urine does not contain nearly so much of the latter as in normal circumstances, indicating that the blood and the tissues retain it with great tenacity; but it is remarkable that in these circumstances the animal may retain its health for a considerable time. Voit has shown the importance of common salt in the phenomena of diffusion,

by the following interesting experiment: If albumen alone be injected into the abdomen of an animal, it is not absorbed, but if it be mixed with a little common salt it is taken up with readiness. Common salt is also necessary in the food of herbivora. It has been supposed that a part of the chloride of sodium undergoes chemical changes in the body, such as supplying chlorine to form the free hydrochloric acid of the gastric juice; but this has not been satisfactorily demonstrated.

The salts of *potash* are also essential in food. They exist in considerable quantity in the blood corpuscles, muscular fibre, and nervous tissue, whilst those of soda are found principally in the fluids. Kemmerich fed two dogs for six weeks with the same quantity of meat entirely deprived of salts. In one case he added to the food a little common salt alone, and in the other case, in addition to the common salt, he gave the salts of potash: at the end of the time, the first dog, which received in its food common salt only, was feeble and extremely emaciated; whilst the other, which received salts of potash in addition, was in vigorous health. In small doses, they encourage the activity of the circulation by increasing the blood pressure, and augmenting the force and frequency of the cardiac contractions. Beyond a certain point, however, they lessen the activity of the circulation.

The salts of *lime* are also required for the nutrition of the textures, more especially for such tissues as bone and teeth. Phosphate of lime, which is the principal salt, is introduced both in articles of food and in water, but the processes by which it is separated from these and incorporated into the tissues, are unknown.

The alimentary importance of salts of *magnesia*, and of *carbonates* and *sulphates* of the alkalies and alkaline earths, although these substances are found in the body, is quite unknown.

Iron exists in the colouring matter of the blood, of which it is an essential constituent. It has been estimated that the amount of iron in the body of an adult is about 3 grammes. When a person is in a condition of constant pallor, called anæmia, it is generally supposed that there is a deficiency of iron in the blood, which is probably the case, as such persons frequently recover colour on the medicinal administration of iron.

The following table shows the quantity per cent. (making allowance for errors of analysis) of mineral matters in the ashes of certain articles of diet:—

Mineral Matter.	Milk.	Beef.	Liebig's Extract.	Egg.	Wheat.	Potatoes
Potash, ...	23·46	39·40	48·12	19·28	27·04	54·21
Soda, ...	6·96	4·86	10·45	6·58	0·45	...
Lime, ...	21·34	1·80	0·23	8·26	1·97	3·35
Magnesia, . . .	2·20	3·88	1·96	2·45	6·60	13·58
Chloride of Sodium,	4·74	1·47	...	24·21	...	2·41
Oxide of Iron, .	0·47	1·00	Traces	1·42	1·35	...
Phosphoric Acid,	38·04	46·74	38·04	26·66	62·59	11·91
Sulphuric Acid, .	0·05	0·30	0·27	1·70	...	6·50
Silica, ...	0·06	...	...	0·45	...	7·17
Carbonic Acid, .	2·50	...	...	9·67	...	...
Total, . . .	99·82	99·45	99·07	100·68	100·00	99·13

3. *Carbohydrates.*—These consist of starch, cane sugar, grape sugar, cellulose, gums, and mucilage. *Starch* forms the chief ingredient of many articles of food, such as potatoes, rice, tapioca, arrowroot, and the products of the cereals and of leguminous plants. It exists in the form of small somewhat oval grains, exhibiting a series of transverse curved markings, as if they were composed of concentric layers. These grains are of various sizes, and they also appear to possess different degrees of resistance to the penetration of

water, an important point as regards their value in alimentation. *Cane Sugar*, familiarly known as obtained from sugar cane or beetroot, exists also in many vegetables frequently used in diet, such as carrot, turnip, parsnips, melon, parsley, cucumber, &c. *Grape Sugar* is found in fruits, honey, and in such fermented liquids as wine, beer, cider, perry, &c. It is important to note that a substance identical with it may be found after death in the liver, which is probably derived, as will be seen hereafter, from a kind of animal starch, called glycogen, formed in that organ. In the muscles, also, more especially in the heart, a small amount of inosite, or muscle-sugar, is found. *Cellulose*, forming the walls of vegetable cells, is of very little use in alimentation, whilst the *gums* and *mucilages* appear to a certain extent to assist in the process.

4. *Fat.*—As this substance is used in food, it consists of a mixture of stearine, palmitine, and oleine. When the latter predominates, the fat is fluid, and exists as an oil; but when the former two are in abundance, the fat is solid, as in lard or butter. When oils are used as articles of diet, they are usually derived from plants, such as olive oil, &c., whilst lard and butter are of animal origin.

5. *Albuminates.*—As examples of these we have gluten, as found in the cereals, and legumen, which, as before stated, is identical with caseine, in peas, beans, haricots, &c. Albuminous matters do not exist to the same amount in plants as in animals. They are met with in animal substances in the form of the myosine of muscle, the caseine of milk, the albumen of eggs, the albumen of blood, the fibrine of blood, &c. As all of these proximate principles contain nitrogen, they are frequently grouped under the term of *nitrogenous*.

In addition to water, salts, carbohydrates, fats, and albuminates which are found, more or less, in every article of diet fitted for the nourishment of the healthy body, various substances are employed by man which may be regarded as *accessories* to food. Such are alcohol, as contained in wines, spirits, beer, &c., vegetable acids, essential oils, condiments, and beverages containing alkaloids, namely, tea, coffee, cocoa, &c.

With regard to *alcohol*, its exact influence, when taken in moderation by those who use it as an article of diet, cannot, in the present state of our knowledge, be precisely stated. It has been asserted by several observers that alcohol is eliminated from the body as alcohol by the various excretory channels. The evidence of this is very doubtful, and it is probable, judging from the analogy of its mode of action with that of other active agents which are known to be decomposed in the body, that it is split up into simpler compounds. So far as mere alimentation is concerned, there can be no doubt that in small doses it acts in the first instance as a local excitant of the digestive mucous membrane and afterwards as a diffusible stimulant upon the circulation and central nervous system. In some cases, it may aid the digestive process both directly and indirectly; but in a state of health it is not only not required, but its use, except in small doses, is positively prejudicial.

The various vegetable acids, which are taken as *condiments* in the form of vinegar, acid fruits, lemonade, ginger wine, ginger beer, clarets, &c., excite a special gustatory sensation which may for a time relieve thirst and even stimulate appetite for solid food. When taken in moderation along with food, they may stimulate the secretion of saliva and of gastric juice. In passing through the body, these acids are, for the most part, converted into carbonic acid, and consequently appear in the form of carbonates in the urine.

The condiments in general use, such as pepper, mustard, ginger, &c., when taken in small quantity, act as local excitants of the mucous membranes of the mouth and of the stomach. By thus promoting a flow of saliva and of gastric juice, they may assist in the process of digestion; but, at the same time, it is to be remembered that perfect digestion may be performed without their use, and that consequently they are not essential articles of diet.

Tea, Coffee, &c.—The influence of tea, coffee, cocoa, &c., will be referred to in treating of the drinks used by man.

2. Composition of Articles of Food.

The nutritive value of different articles of food depends (1) on their digestibility; and (2) on the amount they contain of the proximate constituents which are required for nourishing the body. There are great differences in the percentage composition of food, as may be seen on studying the following table:—

Nature of Food,	Water.	Albumen.	Starch.	Sugar.	Fats.	Salts.
Bread,	37	8·1	47·4	3·6	1·6	2·3
Wheat Flour,	15	10·8	66·3	4·2	2·0	1·7
Oatmeal,	15	12·6	58·4	5·4	5·6	3·0
Rice,	13	6·3	79·1	0·4	0·7	0·5
Potatoes,	75	2·1	18·8	3·2	0·2	0·7
Peas,	15	23·0	55·4	2·0	2·1	2·5
Milk,	86	4·1	...	5·2	3·9	0·8
Cheese,	36·6	33·5	...	...	24·3	5·4
Beef,	51	14·8	...	...	29·8	4·4
Pork,	39	9·8	...	...	48·9	2·3
Poultry,	74	21·0	...	...	3·8	1·2
White Fish,	78	18·1	...	...	2·9	1·0
Egg,	74	14·0	...	...	10·5	1·5

With the aid of this table, the student should contrast the composition of bread with rice, bread with potatoes, bread with cheese, bread with beef, potatoes with beef, and potatoes with cheese, so as to see how one article of food may act as the complement of the other in framing a dietary. He will see that rice and potatoes are rich in starch but poor in albumen, and that consequently they may be combined advantageously with beef, pork, poultry, fish, or cheese, where the reverse is the case. Again, he should note the composition of milk and of egg, both of which may be regarded as typical foods, as they are primarily intended for the nourishment of the young animal.

3. Food as artificially prepared by Man.

Having stated the general composition of the articles of food, more special attention may be shortly directed to the nutritive value of animal and vegetable alimentary substances as prepared by man, and to the various drinks used in civilized countries.

Alimentary substances are rarely in a natural condition suitable for consumption, but they require in the first instance to be prepared by cooking, which transforms them in such a manner as to render the action of the digestive fluids more easy and certain, while at the same time sapidity or flavour is given to the dish. Water, heat, and condiments are the principal agents employed in the preparation of food. Water softens insoluble matters, whilst it dissolves all those which are soluble, as in soups. Heat affects alimentary matters, and according as it is applied quickly or rapidly, or is obtained from an open fire, from vapour, or from a salt infusion, food acquires different characters which please the taste and thus promote alimentation. Cooking separates assimilable from non-assimilable matters; it renders the food more accessible to the digestive fluids; it fits the salts and other soluble matters of food for rapid absorption; it may also condense alimentary substances into a small volume, as in concentrated beef-tea; and, finally, the condiments employed in cooking gratify the taste, and excite the digestive secretions.

Butcher meat may be prepared by roasting, stewing, or boiling. Whatever may be the mode of cooking, the internal temperature of the meat ought not to pass 70° C., nor fall below 56° C. When meat is roasted before an open fire, it is acted upon by a strong heat which, by coagulating the albumen, forms a hard layer on the substance, thus preventing the escape of the juices of the meat. By roasting, meat loses, as a rule, about 20 per cent. of its weight. When beef is boiled in water, about 80 per cent. of the salts are at once dissolved out, and in the fluid various extractive matters, such as creatine, creatinine, &c., are also found. Any gelatine present in the meat is also dissolved. The flesh of young animals contains more of this substance than those of old animals: according to Liebig, 1,000 parts of beef yield 6, whilst 1,000 parts of veal yield 50, parts of gelatine. *Beef-tea* ought to be prepared by placing the meat in cold, and not in hot water, and afterwards gradually heated. If placed directly in hot water, a superficial layer of coagulated albumen is formed, which prevents the escape of the juices of the meat and of the soluble substances, and consequently the beef-tea thus obtained is very poor. If beef-tea be prepared properly, it consists of a solution of gelatine, of salts, and of extractive matters, a little soluble albumen, and any fat which may have been mechanically set free by the process of heating. It may be made more nutritious by the addition of gelatine, bread crumbs, or of bone. There can be no doubt that beef-tea has a certain nutritive value, regarding the exact nature of which, however, considerable controversy has taken place, some supposing that it is due to the extractive matters, whilst others hold that it is really due to the gelatine and salts. The probability is that the stimulating effect produced by a cup of beef-tea after fatigue is due to the extractive matters, and that any nourishment obtained from it is owing to the gelatine, albumen, and fat. *Liebig's extract of meat,* now largely used in the sick-room, consists chiefly of extractives and of the various salts, of which those of potash, as may be seen by referring to the table on page 214, exist in largest amount. This substance ought therefore to be regarded chiefly as a kind of stimulant which acts specially upon a fatigued nervous system; but along with meat-juice, bread, or rice, it is an important adjunct to a nourishing diet. *Salt meat* loses a portion both of organic and inorganic soluble materials, which pass out into the brine. In particular, it loses a large proportion of the salts of potash, which are of high alimentary importance. This may be seen by studying the following table:—

In 100 Parts of Ash.	Pork.		Beef.	
	Fresh.	Salt.	Fresh.	Salt.
Potash,	37·39	5·30	35·94	24·70
Soda,	4·02	...	...	...
Magnesia,	4·81	0·54	3·31	1·90
Lime,	7·54	0·41	1·73	0·73
Potassium,	...	1·25	5·36	...
Sodium,	0·40	34·06	...	16·82
Chlorine,	0·62	53·72	4·86	30·95
Oxide of Iron,	0·35	...	0·98	...
Phosphate of Iron,	...	0·10	...	1·04
Phosphoric Acid,	44·47	4·71	34·36	21·41
Sulphuric Acid,	...	0·12	3·37	0·62
Silica,	...	...	2·07	0·20
Carbonic Acid,	...	...	8·02	...
Total,	100·0	100·21	100·00	99·37

Alimentary substances from the *vegetable* kingdom present great differences in their composition. Leguminous plants are very rich in albuminoids, of which they contain, on an average, about 25 per cent. The cereals, which include such plants as wheat, barley, oats, indian-corn, &c., are rich in starch. The first three, however, contain a considerable quantity of albuminous matter. The cereals are usually prepared in the form of bread, and the process of baking is intended to render the starch more digestible by the previous action of heat, moisture, and fermentation. Potatoes contain a very large percentage of water, and the remainder consists chiefly of starch. Such substances as asparagus, celery, artichokes, carrots, and turnips, contain a large amount of water and a small quantity of albuminoids and carbohydrates. The majority of fruits abound in grape-sugar, various vegetable acids, and water.

The *drinks* used by mankind may be divided into alcoholic, saccharine, acidulated, gaseous, and infusions of various substances, such as tea, coffee, &c. The following table gives the percentage of alcohol in the more common kinds of wines, spirits, and malt liquors in use :—

Brandy, . . .	50 to 60	Clarets, ...	9 to 13
Whisky, . . .	50 ,, 60	Hocks, ...	6 ,, 16
Rum, ...	60 ,, 77	Madeira, . . .	16 ,, 22
Gin, ...	49 ,, 60	Porter, ...	8 ,, 10
Port, ...	16 ,, 23	Bass's Beer, . .	8 ,, 10
Sherry, . . .	16 ,, 25	Table Beer, . .	2 ,, 5
Champagne, . .	5 ,, 13	Sweet Ale, . . .	7 ,, 9

In addition to alcohol, many wines contain colouring matter, organic acids, such as malic and tartaric acids, tartrate of potash, acetic and œnanthic ethers, and carbonic acid; and the peculiar quality of the wine depends upon the predominance of one or other substance. Thus, sherry and madeira contain various ethers, and alcohol; port abounds in astringent matter; hocks contain acids; and the sparkling wines, such as champagne, contain ethers, saccharine matter, and carbonic acid. Brandy contains, in addition to alcohol, œnanthic and other ethers; the aroma of rum depends on butyric ether; gin contains oil of juniper and other aromatics; and whisky, when free from fusel-oil, owes its flavour to something derived from malt or from peat smoke. Malt liquors contain alcohol, sugar, dextrine, gluten, various matters extracted from hops, which give bitterness and an aromatic flavour, and various mineral salts. Certain wines and malt liquors contain a considerable percentage of the salts of potash. Saccharine and acidulated drinks owe their properties to sugar, and to the acids which they contain, of which, in effervescing fluids, carbonic acid is the chief.

It is remarkable that, in different parts of the world, mankind have for ages been in the habit of drinking infusions of certain herbs, all of which contain essentially the same active substance or alkaloid. Thus the tea of China, the coffee of Arabia and the East, the cocoa of South America, the maté or tea of Paraguay, and the guarana of Brazil, have all become valuable beverages, and all contain an active principle, represented by the general formula $C_8H_{10}N_4O_2$, to which the various names of Theine, Caffeine, Theobromine, Guaranine have been given. Infusions of these herbs contain other substances which play an important part in their physiological action. Thus, coffee is rich in aromatic matter; tea contains a considerable amount of tannin and potash salts; whilst cocoa abounds in fatty matter and vegetable albumen. The two first stimulate the nervous system without producing any period of after-depression such as follows alcoholic stimulants. They also increase generally the activity of all the secretions; and, according to some authorities, they diminish the amount of nitrogenous matters separated by the kidneys, indicating that they may possibly lessen the activity of waste of tissue. One of their most remarkable characteristics is the almost instantaneous relief they give to feelings of fatigue, a property which is strikingly manifested in the use of the leaves of coca (a plant of South America containing an alkaloid cocaine, closely resembling theine), which enable the inhabitants of that part of the world to perform fatiguing marches lasting many hours without food. Cocoa, from the fat and albuminous matter it contains, is a highly nutritious substance, but is only to a slight extent a nervous stimulant.

Consult as to physiological action of these active principles, WOOD'S Therapeutics, page 198; also, researches by the AUTHOR, published in a Report on the Antagonism of Medicines, made to the British Medical Association, which contains an account of an investigation by A. HUGHES BENNETT on the action of Cocaine.

4. THE RELATION BETWEEN FOOD AND WORK.

It is evident that the amount of food must have some direct relation to the work done by the individual. Hard work means expenditure of matter and energy, and these must be supplied by food. The following table shows the quantity in ounces avoirdupois, of the different materials of dry food required under different circumstances:—

Nature of the Diet.	Nitrogenous Matter.	Fat.	Carbohydrates.	Salts.	TOTAL.
Bare subsistence diet,	2·33	0·84	11·69	...	14·86
Adult in full health, with moderate exercise, ...	4·215	1·397	18·960	0·714	25·286
Active artizan, not over-worked, ...	5·41	2·41	17·92	0·68	26·42
Hard working labourer, navvy, ...	5·64	2·34	20·41	0·68	29·07

Add to each of these from 60 to 80 ounces of water, taken either alone or as part of the food in a succulent or cooked state. Thus it would appear that in ordinary life, and with a fair amount of labour to perform, a healthy adult requires daily about 28 or 30 ounces of dry nutritious food, along with about 70 ounces of water.

5. Influence of Sapidity.

It must be remembered, however, that a *mixture* of the constituents of food is essential to the formation of a nutritious diet; and, moreover, that there must always be a certain amount of *sapidity* or *flavour* in the food. We should turn with disgust from a mess consisting of these constituents, even in proper proportions, if it were not properly cooked. The best example of a natural food is milk. It contains water, albumen in the form of casein or cheese, fat in the form of butter, sugar, and various salts. Hence it is nature's food for all young animals of the mammalian group.

6. Effects of Climate on Nature of the Food.

The amount and nature of the food required is also affected by (1) the amount of oxygen in, and the temperature of, the atmosphere; and (2) the activity of growth. Exercise and exposure to a cold, bracing atmosphere sharpen the appetite, and thus lead to more food being taken. In cold climates, there is a greater demand for the production of internal heat; and, consequently, one would anticipate that the food consumed would be of such a nature as would produce, on oxidation by the oxygen of the air, a large amount of heat. The substances used as food by man which are readily oxidised are carbohydrates and fats. Carbohydrates contain a sufficient quantity of oxygen to combine with the amount of carbon and hydrogen existing in them, whereas the amount of oxygen in fat is not nearly sufficient for this purpose. Hence it has been supposed that the oxidation of fats by the oxygen introduced in respiration must produce more heat than the oxidation of carbohydrates, and this has been offered as an explanation of the fact that in cold climates the inhabitants instinctively consume a large amount of fatty matter; whereas, in warm climates, they live principally upon carbohydrates.

7. CONDITIONS OF A HEALTHY DIET.

A healthy diet must fulfil the following conditions:

1. It must contain a due proportion of the various proximate principles found in the body of man.
2. It must have a certain sapidity or flavour which will render it palatable and thus indirectly promote the digestive process.
3. It must be adapted as regards quantity and quality to the amount of work done by the individual.
4. It must be adapted as regards quality to the climate.

Various interesting observations have been made which show that animal life cannot be maintained by the use of one proximate principle alone, a few of which may be shortly narrated. Magendie fed dogs upon sugar, oil, gum, or butter alone, and found that for one or two weeks they did very well, but after that became weak, and died on the thirty-second or thirty-sixth day. When they were fed on white bread and water, they lived fifty days; when on cheese and white of egg, they lived longer, but became feeble, emaciated, and lost their hair. The experiments by Edwards and Balzac have shown that a diet of bread and gelatine is insufficient, producing death after emaciation, without appreciable lesion. The addition of brown soup, however, renders bread and gelatine highly nutritious. Dr. Hammond limited himself to 1½ lbs. of gum on one occasion, and a like quantity of starch on another, with water, per day. Hunger, debility, and fever became so great that he was obliged to abandon the first diet on the fourth and the second on the tenth day. When, instead of these substances, he took 1½ lbs. of albumen—diarrhœa, albuminous urine, and disgust at the food obliged him to abandon it on the ninth day. Of all the articles of food, milk appears to be that which contains the proximate principles in the best proportions. A like result may be obtained by other articles together, such as fat pork with veal, potatoes with beef, and rice with mutton or fowl. Again, stuffing is generally added to ham and veal, bacon to beans, ham to fowls, and so on. The addition of butter to bread is the almost universal food of the nursery. Mankind have for the most part adopted these rules instinctively. Persons who feed principally on flesh prefer it fat; and those who live largely on vegetables, as potatoes and rice, take considerable quantities of milk. The same result is obtained by the use of fermented liquors. Hence bread and wine constitute a diet resembling milk in chemical constitution. (*Hughes Bennett.*)

Consult Pavy on Food; and Parke's Hygiene. Both of these works are of the highest order, and ought to be familiar to every medical man, as they contain all the facts relating to food and dietetics. Dr. Pavy's work is the best authority on scientific dietetics in our language.

Hunger and Thirst.

The sensation of *hunger* is referred to the stomach, and it may be at least temporarily relieved by introducing into that organ even matter that is not nutritious. Hence it would appear that in some way it depends on an excitation of the sensory nerves of the stomach and possibly of other portions of the intestinal canal. On the other hand, it is well known that the sense of hunger may be appeased by introducing nutritious food into the small intestine, and by taking nutritious substances, such as solutions of peptones, highly concentrated and so small in bulk as to distend the organ only to a slight degree. The latter facts indicate that hunger may be the result partly of impressions derived from the stomach and partly of a fusion of indefinite sensations caused by impressions from organs partially exhausted from a want of nutritious matter. Alcohol, tobacco, and various narcotics frequently diminish and restrain for a considerable time the acuteness of feelings of hunger, and it is also well known that certain psychical states have the same effect. In these instances, the influence is probably exerted upon the central, and not the peripheral, origin of the nerves of the stomach.

Thirst is a purely local sensation resulting from a dry condition of the mucous membrane of the posterior wall of the pharynx, which is supplied with filaments from the pneumo-gastric, glosso-pharyngeal, and trigeminal nerves. When the dry condition is removed even by occasional moistening, thirst is for the time relieved. The dryness may result either from a general diminution of the amount of water of the blood; from the action of certain substances, such as atropine, which arrest secretion from mucous surfaces; or from a mental state of fear or excitement. The sensation may be removed by the direct injection of water into the blood, or into the alimentary canal, or even temporarily by immersion of the body in water. It may be remarked that experiments on animals have not yielded any definite information as to the conditions of hunger and thirst.

The length of time a human being may exist without food or drink cannot be very precisely stated, as it is evident that much will depend on the amount of waste going on in the body during the time, the amount of oxygen in the air, and the surrounding temperature. In some circumstances, men may pass into a condition somewhat similar to the hybernating state of certain animals, when the amount of waste going on in the body is reduced to a minimum. Thus Indian Fakirs, under the influence of opiates or of Indian hemp, have remained without food, in a state of trance, for even six weeks. Under ordinary circumstances, complete abstinence from food and drink cannot be supported beyond the eighth or tenth day. With a supply of water, life may be prolonged for a considerable time even with an exceedingly small quantity of solid food, and it is an undoubted fact that an animal will live longer upon water alone than on any other proximate principle of food in a dry state. The complete deprivation of water will usually destroy life in eight or ten days, and even after the third day its absence is the cause of horrible distress. In treating those who have unhappily been the subjects of starvation, it is important to remember that the want of food has impaired the powers of digestion as well as the powers of locomotion, and therefore, in these circumstances, food should be given at first in the fluid form and in small quantities. As the stomach recovers power, the amount may be slowly increased and solid food given with care and moderation.

Individuals are met with occasionally who have an excess of appetite, a condition termed *Bulimia*. This may occur in certain diseases, as for instance, in Diabetes, and it is frequently seen in the convalescent stage of fevers. In some rare instances, it appears to be the normal state of the person. Thus Captain Parry, the celebrated Arctic explorer, narrates an instance of an Esquimaux who, on one occasion, and apparently as a common exploit, in twenty-four hours, devoured 35 lbs. of meat and a number of tallow candles. A still more remarkable case is that of Tarrari, a French soldier, whose appetite was so voracious as to lead to his dismissal from the army. Tarrari's case was one of undoubted disease, and it is remarkable that he died an emaciated miserable man, but with an undiminished appetite.

On the other hand, the minimum quantity of food required by each individual, in the performance of the active duties of life, cannot be precisely stated, as much depends on idiosyncracies of constitution and on habit. Many men have led active lives on comparatively small quantities of food, and, judging from the great prevalence of diseases of the digestive organs, it is highly probable that many persons consume more food than they require. Improper food, excess of food, and irregularity in taking food, are the most common causes of dyspepsia, and of other forms of gastric derangement.

As the food passes along the digestive canal, it is submitted to various movements, and to the chemical and physical actions of various fluids. It is most convenient to study these operations in their natural order, according to the cavity in which they take place.

It is presumed that the student has made himself familiar, during his anatomical studies, with the structure of the teeth, the muscles moving the jaws, or muscles of mastication, and with the general form, position, and relations of the digestive organs.

A.—CHANGES IN THE MOUTH.

Some animals introduce solid food into the mouth by the action of the tongue, as in the ox, or by the mobility of the lips, as in the horse, or by a proboscis or trunk, as in the elephant, or with the aid of the fore paws, as seen in squirrels and monkeys. Man carries food to the mouth with the hand. Fluids may be poured into the mouth, and from thence pass directly into the pharynx, and through it, by a process of deglutition, into the stomach. Usually, fluids are sucked into the mouth by a kind of aspiration. In drinking from a cup, with the lips immersed, the air is removed from the mouth by inspiring, and the fluid flows in; when the lips are not entirely immersed, some air rushes in with the fluid, and a gurgling sound is produced. When a child sucks at the breast, the mouth acts as a kind of pump, of which the tongue is the piston. The lips are applied hermetically around the nipple, the isthmus of the fauces is closed by the base of the tongue touching the soft palate, and the anterior part of the tongue is placed below the nipple. When these arrangements are made, there is muscular action of the cheeks, lips and tongue, which aid the pressure of the atmosphere on the breast in forcing the milk into the cavity of the mouth. No respiratory effort requires to be made, and hence a child breathes quietly while the mechanism of suction is going on.

After food is introduced into the mouth, it is there subjected to two processes which are carried on simultaneously. It is broken down by the triturating movement of the jaws, and it is mixed with a fluid poured into the mouth by various glands.

1. Mastication.

The food is divided by the incisor and the canine teeth, and is then triturated between the superior and inferior molars. The hard surfaces of the teeth, formed of enamel, covering the pointed crowns of the canines and the tubercules on the molars, enable the teeth to act forcibly, even on very hard substances, without much risk of injury, whilst the delicate sensibility of the teeth enables us to graduate the amount of pressure required. The lower jaw may be moved, with reference to the upper, either from above downwards or horizontally. The first movement approximates and separates the dental arches, whilst the second produces a to-and-fro movement of trituration. These movements depend anatomically on the form of the articulation between the condyle of the lower jaw and the glenoid cavity of the temporal bone. In carnivora, the form is such as to permit chiefly of vertical movements, as these animals do not masticate their food, but usually swallow it in lumps. A different form of articular surface, permitting of gliding movements in the horizontal direction, exists in herbivora, so as to render possible the extensive lateral movements of the lower jaw in chewing the cud. Man, who is omnivorous, possesses a mechanism admitting, within certain limits, of both kinds of movements. The lower jaw may be pulled down by the genio-hyoid, the mylo-hyoid, and the anterior belly of the digastric, all of which are muscles passing from the lower jaw to the hyoid bone, which is fixed during the movement in question by the omo-hyoid, thyro-hyoid, and sterno-hyoid muscles. The lower jaw is raised by the masseter, the temporal, and the internal pterygoid. When the two pterygoids on each side act together, the lower jaw is pushed forwards, and when the external pterygoid acts on one side, the jaw is moved horizontally to the same side, as occurs in the grinding movements of mastication.

In mastication, the food is rolled backwards and forwards, and from side to side, by the movements of the tongue, an organ which, by the action of its extrinsic muscles, may be moved as a whole in all directions, while its intrinsic fibres permit of a change of form to suit every varying condition. The tongue also assists in the process as a tactile organ, by which we become conscious of the position of the bolus of food with reference to the teeth, and also by which there is an almost instinctive knowledge that the food is in a fit state for deglutition.

The *motor* nerves concerned in mastication are: (1) the motor branches of the fifth, supplying the muscles of mastication and the anterior belly of the digastric; (2) the hypoglossal, governing the movements of the tongue; and (3) the buccinator branch of the facial. The *sensory* nerves belong chiefly to the fifth; and the *centre*, associated with reflex movements, is in the medulla oblongata.

2. INSALIVATION.

During the process of mastication, the food is mixed with a fluid, termed the *saliva*, which is secreted from three pairs of glands, namely—the parotid, submaxillary, and sublingual. The union of the secretion of these glands, along with a small quantity of fluid supplied by numerous glands found under the lining membrane of the lips and cheeks, constitutes the mixed saliva, of which from 2 to 3 lbs. may be secreted daily.

1. *General Physical and Microscopical Characters of Mixed Saliva.*—This is a transparent or slightly opalescent fluid, which deposits a small amount of sediment on being allowed to stand for a time in a conical vessel. On examining a small portion of the sediment with a magnifying power of 350 diameters, it is found to contain squamous epithelium cells, derived from the mucous membrane of the mouth, and globular nucleated cells, in which movements may be distinctly seen, obtained from the salivary glands. The latter cells are termed *salivary corpuscles*. In addition

FIG. 43.—Drop of Saliva, showing, *a*, pavement or squamous epithelium from mouth; and *b*, salivary corpuscles.

to these, larger masses of protoplasm, exhibiting amæboid movements, are sometimes met with.

2. *Chemical Characters of Mixed Saliva.*—Mixed saliva is alkaline, from the presence of the alkaline phosphate of soda. It contains about 5 per 1000 parts of solid matter. The solids consist of *inorganic* substances, such as carbonate of lime, alkaline chlorides, the phosphates of lime and of magnesia, and a small quantity of sulpho-cyanide of potassium. It also contains some carbonic acid, and traces of oxygen and nitrogen (see table, p. 44). The *organic* materials consist principally of a special substance, termed *ptyaline,* which has the remarkable property of converting starch into sugar. When this substance is obtained tolerably pure, it is a greyish white powder, readily soluble in water. It belongs to the class of ferments, and it transforms starch into glucose or grape sugar with great rapidity. In addition to ptyaline, the saliva contains mucus, albumen, and globuline. The following table shows the results obtained by the analysis of the mixed saliva of man in three cases :—

In 1000 Parts.	Berzélius.	Frerichs.	Jacubowitch.
Water,	992·9	994·10	995·16
Solid Matters,	7·1	5·90	4·84
Ptyaline,	2·9	1·42	1·34
Mucine,	1·4	2·13	1·62
Sulphocyanide of Potassium,	...	0·10	0·06
Salts,	1·9	2·19	1·82

3. *General Character of Special Salivas.*—The secretions from the various salivary glands have been carefully collected

and examined, and have been found to present characters peculiar to each.[1] The *parotid* saliva is fluid, limpid, and clear as water. Its reaction is alkaline, but less so than that from the submaxillary gland. It is very doubtful whether or not it contains any ptyaline. The *submaxillary* saliva is much more viscid, and apparently it contains a larger quantity of mucus. It also contains ptyaline and sulphocyanide of potassium. The more special characters of this saliva will be presently described. The fluid obtained from the *sublingual* gland is transparent, and extremely viscid, from the quantity of mucus it contains.

4. *Influence of the Nervous System on Salivary Secretion.*—The influence of the nervous system on glandular secretion has been so clearly elucidated in the case of the submaxillary gland of the dog, as to merit the careful attention of the student at this period of his physiological studies, and therefore it must be described somewhat more in detail than will be necessary with reference to the other secretions.

The following brief account of the results of experimental investigations into the functions of the submaxillary gland will be understood with the aid of the diagram in Fig. 43. This gland receives nerve fibres from three sources, namely, from the facial, from the submaxillary ganglion, and from the cervical sympathetic. The chorda tympani, which is a branch of the facial, joins the trunk of the lingual nerve for a short distance, and then leaves it to ramify in the gland. In the angle which it thus forms with the lingual lies the submaxillary ganglion above mentioned. From it, fibres originate which reach the gland along with the chorda.

---

[1] The general methods by which saliva and the other fluids of the body may be examined will be described in a small work by the author, in course of preparation, entitled "Lessons in Practical Physiology."

The sympathetic fibres are derived from the superior cervical ganglion. (*Lauder Brunton.*)

When a canula is placed in the duct of the submaxillary gland, there flows from it a somewhat turbid, whitish fluid. On applying weak acids to the tongue, the saliva becomes more limpid, whilst, on applying alkalies, it is somewhat turbid, white and viscous. It has been found experimentally that these characters may be more or less changed according to the nerve stimulated. Thus:—

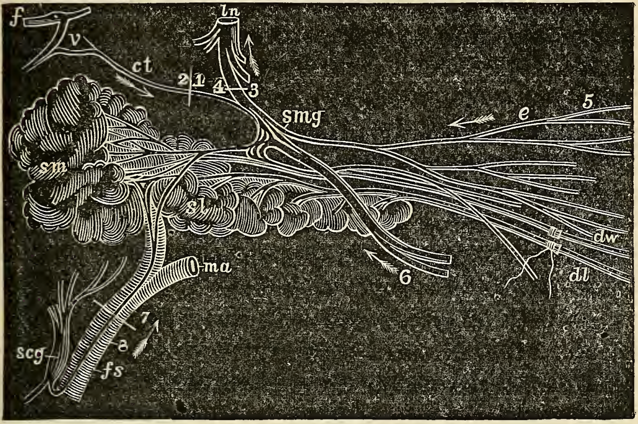


Fig. 43.—Diagram showing the nervous arrangements of the submaxillary glands of the dog: *s m*, submaxillary gland; *s l*, sublingual gland; *d w*, Wharton's duct, from the submaxillary gland; *d l*, duct of the sublingual gland; *f*, facial nerve; *v*, vidian nerve; *c t*, chorda tympani, joining the lingual branch of the 5th *l n*; *s m g*, submaxillary ganglion; *s c g*, superior cervical ganglion of the sympathetic; *f s*, filament from the sympathetic, passing upwards to join the submaxillary ganglion *s m g*; *l*, sensory branches of the lingual, distributed to the mucous membrane of the mouth; *m a*, deep maxillary artery; the figures refer to the points of section of the various nerves, and the arrows indicate the normal direction of the nerve current.

1. If the chorda be now irritated at 1, the arteries of the gland dilate, the stream of blood through them becomes more rapid, the veins pulsate, and the saliva discharged from the duct is copious and watery. This variety may be termed

the *saliva of the chorda tympani*. It contains very few histological elements, and consists principally of water, holding in solution a very small quantity of the various salts.

2. When the sympathetic fibres are excited, the arteries contract, the stream of blood becomes slower, the veins contain very dark blood, and the secretion, called *saliva of the sympathetic*, is ropy, viscous, opaque, and contains numerous histological elements, such as salivary corpuscles, and the protoplasmic masses already alluded to.

3. If the lingual branch of the 5th be divided below the anastomosis of the chorda and the sympathetic, certain stimuli, such as feeble electric currents, or the vapour of ether, applied to the tongue, cause a discharge of saliva, *saliva of submaxillary ganglion*, which stops immediately on dividing the lingual between the gland and the submaxillary ganglion. The properties of this variety have not been carefully examined.

4. If the lingual be divided at 4 — 3, and a stimulus be applied to the end next the brain, there is a copious secretion, but this is not the case if the chorda tympani has been previously divided at 1. This would indicate that there is a nervous arc, consisting of sensory filaments in the lingual, a nerve centre somewhere in the encephalon, and secretory filaments in the chorda,—an example of what may be termed a reflex excito-secretory action. If, after division of the lingual, the chorda, and the sympathetic, stimulants be applied to the mucous membrane of the mouth, there is still an increase of secretion, a fact which can only be explained by supposing that the submaxillary ganglion acts as a subsidiary reflex centre (*Claude Bernard*).

Ludwig was the first to show clearly that the increased secretion produced by excitation of the chorda is immediately dependent on increased activity of the function of the secreting elements of the gland, and not on changes in the bloodvessels; in other words, that in the submaxillary gland the process of secretion is not a mere filtration, but is effected by changes which go on within the gland itself, of such a nature as to determine a current from the circulating blood towards the duct. This conclusion was based by Ludwig on the observation,—first, that if the duct be constricted, secretion continues, notwithstanding that the pressure in the interior of the gland is greater than that in the arteries; and, secondly, that secretion continues after circulation has ceased; *e.g.*, after the head has been severed from the body. (*Lauder Brunton*). In connection with this view it is important to note that Pflüger asserts that the terminations of nerves may be traced into direct connection with the protoplasm of the salivary cells, and even with their nuclei. He also believes that the cells, both of the alveoli and of the smaller ducts, undergo extensive disintegration during the active state of the gland, and are afterwards renovated. It has also been ascertained that the chorda contains two kinds of fibres, one influencing secretion directly, and the other having an inhibitory action on the bloodvessels. Thus, atropine paralyses the secretory fibres without having any effect on the other kind.

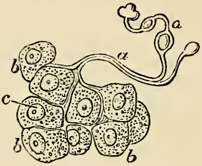


FIG. 45.—Nerves terminating in a cluster of cells in a salivary gland; *a*, nerve; *b*, *b*, *b*, cells; *c*, nucleus; *d*, small swellings on nerve fibres.

From these facts we draw the following conclusions regarding secretion: (1) secretion may be increased by direct action of nervous energy on the protoplasm of secreting cells; (2) secretion may be increased or diminished according to the supply of blood sent to the gland; (3) secretion does not depend simply on a mere filtration of fluid from the blood, but also on cellular activity; (4) the supply of blood to a gland may be under the control of two antagonistic sets of nerve fibres, the one so acting as to increase, while the other diminishes, the supply of blood; (5) the nervous arrangements of secretion may be under the control of a reflex centre or centres in close proximity to the gland, or in the cerebro-spinal axis; and (6) that secretion is attended with an increase of temperature, and is thus one of the sources of animal heat.

Consult regarding structure of salivary glands—QUAIN, vol. II., p. 339. STRICKER'S Hand Book, art. Salivary Glands. And regarding experimental investigations, CLAUDE BERNARD, Leçons sur la Digestion, p. 282. LAUDER BRUNTON, in Hand Book for Physiological Laboratory, p. 469.

5. *Action of Saliva upon Food.*—Saliva acts only upon one proximate principle of food, namely—starch, which it converts, first, into dextrine, and afterwards, with the absorption of water, into glucose or grape sugar. Thus :—

$$\underset{\text{Starch.}}{C_6H_{10}O_5} = \underset{\text{Dextrine.}}{C_6H_{10}O_5} + H_2O = \underset{\text{Glucose.}}{C_6H_{12}O_6}$$

To effect this transformation quickly, the temperature must be about 35° C. When the temperature is less, the action is much slower, and when it rises above 70° C., the action of the ptyaline is at once arrested. The action is much more rapid with boiled than with raw starch.

Consult LAUDER BRUNTON *ut supra*. FOSTER and LANGLEY'S Practical Physiology. Also, for a long and interesting account of the changes occurring in the starch grain, BEAUNIS' Physiologie, p. 379.

The saliva not only effects chemical changes upon the starch, but it favours articulation by moistening the mouth; assists in mastication by softening the food, and thus preparing it for the further action of the digestive fluids; and it facilitates deglutition, or swallowing.

B.—DEGLUTITION, OR SWALLOWING.

Under deglutition is included the steps of the process by which the food is conveyed from the mouth to the stomach. It may be divided into three periods. During the first, the bolus is carried through the isthmus of the fauces; in the second, it passes through the pharynx; and, in the third, it is carried through the œsophagus.

When the bolus arrives at the isthmus of the fauces, an involuntary and reflex movement commences, which it is impossible to stop. The tongue is carried backwards by the contractions of the stylo-glossi and mylo-hyoid muscles; and, at the same time, by the action of its intrinsic fibres, the tongue changes its form, and pushes the bolus from before backwards, against the soft palate. The bolus then passes through the isthmus of the fauces, and the anterior pillars approximate behind it, so as to prevent its return into the mouth.

The bolus having now reached the pharynx, a series of simultaneous movements occur, with the object, on the one hand, of preventing its entrance into the nose, and into the respiratory passage; and, on the other, of carrying it into the œsophagus.

a. *Movements of the Pharynx.*—The lower jaw, having been made a fixed point by the muscles of mastication pressing the dental arches against each other, or against a bolus of food, the pharynx is drawn upwards, and somewhat forwards, by the action of the palato-pharyngei, stylo-pharyngei, the constrictors, and the muscles passing from the lower jaw to the hyoid bone. The ascension of the pharynx is accompanied by a similar movement of the larynx, as may be readily observed by putting the tip of the finger on the larynx during the act of swallowing. At the same time, the constrictor muscles of the pharynx contract from above downwards, so as to carry the bolus towards the œsophagus.

b. *Closure of the Nasal Passages.*—With the view of preventing the regurgitation of the food into the nasal openings, the soft palate is raised and made tense, by the levator palati muscles, the posterior pillars of the fauces are almost completely approximated by the action of the palato-pharyngei, and the small chink left between them is closed by the uvula, containing the azygos uvulæ. The posterior border of the soft palate is thus directed almost horizontally backwards, and nearly touches the posterior wall of the pharynx. In herbivora, such as the horse, the soft palate is so long as to entirely cut off communication, during deglutition, between the pharynx and the nasal passages; and, consequently, regurgitation cannot possibly occur in this animal. In the dog, on the other hand, the soft palate is so narrow as not to shut off communication, so that when this animal is swallowing fluids, a small portion of these is always returned by the nostrils.

c. *Closure of the Respiratory Passage.*—This is effected by closure of the glottis from close approximation of the true vocal cords, and by depression of the epiglottis, due to the action of its proper muscles. These movements may be readily observed with a laryngoscope, an instrument by which the throat is illuminated, and a reflection of the rima glottidis is seen in a small mirror. (*Czermak.*)

The food, being thus prevented from passing into the mouth, the nasal passages, or the glottis, is carried downwards by the contractions of the pharynx into the œsophagus. When it reaches the œsophagus, the pharynx falls downwards, and the three orifices of the mouth, nasal openings, and glottis, are opened, and the bolus is carried from above downwards in the œsophagus by a series of successive contractions. The movement in the œsophagus is wavelike, as may be seen in the neck of a horse drinking water from a trough. Such movements are termed peristaltic. During deglutition, the Eustachian tube is open.

The movements above described are excited by the action of a stimulus, such as a morsel of food or a few drops of liquid, touching the posterior parts of the tongue and the anterior parts of the fauces. It would appear that they are facilitated by the food being slightly moistened, as it will be found almost impossible to swallow a perfectly dry powder. It is also to be noted that it is extremely difficult to perform the movements with the mouth open.

Nervous Arrangements of Deglutition.—Deglutition affords an excellent example of a complex reflex action. Many muscles are involved in the process, and it is evident that they must be co-ordinated, both as regards time and amount of contraction, with the greatest nicety. The *sensory* nerves are branches of the fifth supplying the palate; of the glosso-pharyngeal, distributed to the tongue and pharynx; and the superior laryngeal of the pneumo-gastric, for the upper orifice of the larynx. The *centre* is situated in the medulla oblongata; and the *motor* nerves are the glosso-pharyngeal, supplying the muscles of the pharynx; a twig of the facial distributed to the palato-pharyngeus; branches of the fifth, supplying the palato-glossus, the supra-hyoid muscles, and the muscles of mastication; and, lastly, branches of the pneumo-gastric, sending motor influences to the larynx and œsophagus.

C.—CHANGES IN THE STOMACH.

After the food has reached the stomach, it is subjected, simultaneously, to the following three influences: (1) a temperature of about 40° C., (2) a regular movement by which it is slowly rotated in the cavity, and (3) the physico-chemical action of a special fluid called the gastric juice.

The form of the stomach varies in different animals according to the nature of the food, that of carnivora being simple, whilst that of herbivora is more complicated, as seen in Fig. 46.

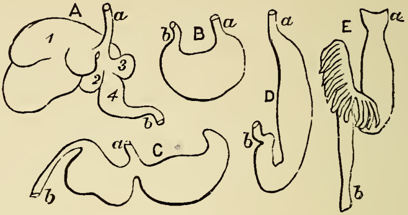


Fig. 46.—Stomachs of various animals; A, sheep; B, hyena; C, hamster; D, seal; E, a salmon; *a*, cardiac opening or lower end of œsophagus; *b*, pyloric opening or beginning of duodenum.

1. Movements of the Stomach.

The wall of the stomach is composed of a serous layer externally, derived from the peritoneum, a mucous coat internally, whilst, between the two, there is a contractile coat, formed of layers of involuntary muscular fibre. Regarding the minute structure of these, reference is made to Quain's Anatomy, Vol. II., p. 349. By slow rhythmical contractions of these muscular fibres, movements are effected.

When the stomach is empty, its greater curvature is directed from above, downwards, but when it is filled, the stomach rotates on its horizontal axis, so as to cause the greater curvature to look forwards and the lesser to look backwards. By this arrangement, the stomach is permitted to dilate in the direction of least resistance, that is, towards the anterior abdominal wall. The food is directed from the cardiac end in two streams, one along the great cul-de-sac and along the greater curvature to the pyloric opening, and the other along the lesser to the same opening. At the pyloric opening, the two streams join to form another current, which passes back to the cardiac opening almost through the central part of the cavity. By these movements the food is thoroughly mixed with the fluids poured into it from the mucous membrane of the stomach. During digestion, the pyloric orifice is firmly closed by the contraction of a strong band of fibres forming a sphincter, which relaxes occasionally so as to permit the passage of digested matter from the stomach into the duodenum. The arrangements by which this relaxation occurs at definite times are unknown.

a. *Mechanism of Vomiting.*

Closely connected with the mechanisms just described is the act of vomiting, which occurs so frequently in various diseased conditions as to merit special attention. Vomiting may be caused: (1) by the introduction into the stomach of an irritating substance, which may act either directly on the stomach itself, or by being absorbed into the blood, may influence reflex centres associated with the movements of the stomach and allied organs (foreign bodies, undigested food, worms, bile, such emetics as mustard, sulphate of zinc, sulphate of copper, &c.); (2) by the action of poisonous substances introduced into bloodvessels or absorbed by the skin, which may influence the stomach directly or the reflex centres above alluded to (injection of tartar emetic into vessels or absorption by inunctions of emetine, apo-morphia, ipecachuan, &c.); (3) by irritations occuring in other organs which appear to influence the reflex centres (pregnancy, abdominal tumours, calculi, passage of gall-stones, &c.); (4) by irritations in the neighbourhood of reflex centres themselves (inflammatory actions at base of brain, as in acute tubercular meningitis); and (5) by psychical conditions, such as feelings of loathing and disgust either on seeing a disagreeable object or even remembering an object which previously excited those feelings. The peculiar kind of vomiting and nausea known as sea-sickness is also associated with nervous arrangements, and will be adverted to in treating of the sense of equilibrium.

Vomiting is usually preceded by a peculiar internal sensation called nausea. The first event is a deep inspiration which, by causing descent of the diaphragm and filling the lungs with air, affords a fixed surface against which the stomach may be pressed, either by its own contractions, or by pressure of the abdominal muscles. The cardiac orifice of the stomach is then opened by contraction of the longitudinal fibres of the œsophagus, and the walls of the stomach contract spasmodically, so as to force the food into the œsophagus, as it cannot escape through the pyloric orifice, in consequence of the sphincter remaining firmly contracted. The matters thus ejected into the œsophagus are carried upwards into the pharynx by an anti-peristaltic movement; sometimes the orifices of the larynx and the nasal passages are closed by the same mechanism as has been described in deglutition, but frequently, in consequence of the violence of the action, matters may be forced into these openings. In violent vomiting, the stomach is forcibly squeezed against the diaphragm and vertebral column by contractions of the abdominal muscles.

Vomiting is readily performed by carnivora, but from the anatomical arrangements it is almost impossible in the horse. *Regurgitation* of food from the stomach occurs as a normal act in ruminants, and human beings are sometimes met with who have this power. *Eructation* is a violent expulsion of gas from the stomach, and causes a sound in the upper part of the œsophagus.

b. *Nervous Arrangements connected with the Movements of the Stomach.*

The nerves which supply the stomach are the pneumogastric and the splanchnic, but their exact distribution is still unknown. Stimulation of the splanchnic nerves or of the sympathetic produces no effect upon the movements, whereas, when the pneumo-gastric is stimulated, vigorous movements occur. As such movements persist for a time, after division of both nerves, there can be no doubt that ganglionic centres exist in the wall of the organ. In the reflex movement of vomiting above alluded to, impressions are conveyed by sensory filaments of the pneumo-gastric to the medulla oblongata, and are from thence transmitted along motor filaments of the same nerve to the stomach, and are also radiated along numerous other nerves to the muscular mechanisms involved in the act.

2. Physical and Chemical Changes in the Stomach.

The mucous membrane of the stomach contains numerous tubular glands. The upper part of these glands is lined by columnar epithelial cells, whilst the lower part contains large, spheroidal, coarsely granular cells, which are called *peptic* cells, as they are believed to be the agents concerned in the secretion of gastric juice, of which from 5 to 6 lbs may be secreted daily.[1] More recently, Heidenhain has attempted to show that in the centre of the gland there are somewhat smaller, angular, or polyhedral, and finely granular cells, which are more specially devoted to this function. There can be no doubt that the columnar epithelial cells of the mouths of the glands secrete mucus, whilst those placed more deeply form the elements of gastric juice. In addition, glands are found more especially in the pyloric region, which,

---

[1] It is useless to attach much importance to the statements made as to the quantities of the various digestive fluids secreted daily. From the difficulty of the observations, and the fact that the amount will probably vary in different persons, and even at different times in the same person, under influences of diet, state of health, &c., it is not surprising that authors should not agree on this subject.

as they are lined throughout with epithelium, similar to that covering the general surface of the stomach between the mouths of the glands, are regarded as mucous glands.

Consult QUAIN'S Anatomy, vol. II., p. 354.

For purposes of experimental investigation, gastric juice has been obtained in various ways. Thus Spallanzani and Reaumur caused animals to swallow a small perforated metallic sphere, in which a bit of sponge was inserted, and which could be withdrawn from the stomach by a thread, or expelled by vomiting. Again, some rare cases have occurred in human beings in which a fistulous opening through the walls of the abdomen into the stomach have become permanent, and in some investigations, permanent fistulous openings have been established in animals. Investigations into the digestive process have also been conducted outside of the body by the use of an artificial gastric juice, obtained by treating the mucous membrane of the stomach of the dog or pig with glycerine, and acidulating the fluid by hydrochloric or lactic acids.

The most famous case of gastric fistula that probably ever occurred, inasmuch as observations made by means of it laid the foundation of our knowledge of the process of digestion (and with which, therefore, every student of physiology ought to be acquainted) is that of Alexis St. Martin, a Canadian, eighteen years of age, who, when in good health, was accidentally wounded by the discharge of a musket on June 6th, 1822. "The charge," says Dr. Beaumont, who, after conducting the case to a successful issue, so far as the life of his patient was concerned, took the man into his employment and conducted a careful and elaborate series of investigations, "consisting of powder and duck shot, was received in the "left side, at a distance of one yard from the muzzle of the "gun. The contents entered posteriorly, and in an oblique "direction, forward and inward, literally blowing off the "integuments and muscle to the size of a man's hand, "fracturing and carrying away the anterior half of the sixth "rib, fracturing the fifth, lacerating the lower portion of the "left lobe of the lung, the diaphragm, and perforating the "stomach." From this injury he gradually recovered; but, 12 months after the accident, a perforation into the stomach, 2½ inches broad, still remained. Subsequently, a small fold of the mucous membrane of the stomach appeared, and gradually increased in breadth, till it filled the aperture and acted as a valve, opening from without inwards. As the man continued in health, here was evidently an excellent opportunity of acquiring information regarding the digestive process in the stomach.

1. *General Physical Characters of the Gastric Juice.*—When obtained pure, it is a limpid colourless fluid, having an odour somewhat like that of old vinegar. Specific gravity, 1005 Under the microscope, it exhibits no well defined histological elements.

2. *Chemical Composition of Gastric Juice.*—It contains about 10 parts per 1000 of solid matter. A free *acid* always exists in gastric juice, which is usually hydrochloric acid, rarely lactic acid alone, and not unfrequently a mixture of both acids. The mineral salts are alkaline chlorides, chloride of ammonia, chloride of calcium, and the alkaline and earthy phosphates. It also contains usually a small amount of albuminous matter, as indicated by the slight opalescence caused by the addition of bichloride of mercury. The principal organic constituent is *pepsine,* a substance belonging to the class of ferments, which, when obtained pure, is a greyish white, amorphous powder, slightly soluble in water, but readily soluble on the addition of acid to the water. It contains nitrogen, but its exact chemical composition has not been determined, probably from the difficulty of obtaining

it pure. It is important, for experimental purposes, to recollect that it is readily given up to glycerine, so that a digestive-glycerine-extract may be obtained by cutting the mucous membrane in small pieces and immersing them in that fluid. The following is an analysis of the gastric juice of man as contrasted with that of the dog and sheep :—

In 1000 Parts.	Man.	Dog.	Sheep.
WATER,	994·40	973·0	986·15
SOLIDS,	5·60	27·0	13·85
Pepsin and Organic Matter,	3·19	17·1	4·05
Chloride of Sodium,	1·46	2·5	4·36
Chloride of Potassium,	0·55	1·1	1·52
Chloride of Ammonium,	...	0·5	0·47
Chloride of Calcium,	0·06	0·6	0·11
Free Acid,	0·20	3·1	1·23
Phosphate of Lime,	0·12	1·7	1·18
Phosphate of Magnesia,		0·2	0·57
Phosphate of Iron,		0·1	0·33

3. *Chemical Action of the Gastric Juice.*—The gastric juice acts only upon albuminous substances, which it transforms into *peptones*, or bodies readily soluble and diffusible, and consequently in a condition permitting of ready absorption into the blood. Peptones are distinguished from albuminous substances by the following general characters :—

1. They are always readily soluble in water.
2. They diffuse through organic membranes with great facility, and their endosmotic equivalent is small.
3. They are not precipitated by boiling, as happens with ordinary albumen.

4. They are not precipitated by mineral acids, nor by the perchloride of iron, sulphate of copper, nor by the majority of metallic salts.
5. When injected into the blood, they do not appear as albumen in the urine.

When more carefully studied, as has been done by Brücke, Meissner, and others, they are found to present various modifications, with the general characters of which the student ought to be acquainted. These are :—

1. *Peptones Proper*—of which there are three varieties, all agreeing in being very soluble in water and in dilute acids, but differing as follows :—
   (a) A. *Peptone*, precipitated from neutral solutions by concentrated nitric acid, and by ferrocyanide of potassium from solutions slightly acidulated with acetic acid.
   (b) B. *Peptone*, precipitated by ferrocyanide of potassium and not by nitric acid.
   (c) C. *Peptone*, precipitated by neither nitric acid nor by ferrocyanide of potassium.
2. *Parapeptones*—These are precipitated from slightly acid or slightly alkaline solutions by a mixture of alcohol and ether; they are precipitated by concentrated solutions of neutral salts, such as sulphate of soda, and the prolonged action of the gastric juice, or boiling, renders them insoluble. The insoluble state has been termed *dyspeptone*.
3. *Metapeptones.*—If a fluid be previously neutralized and any parapeptone present be removed by filtration, the addition of a very small quantity of acid causes a flocculent precipitate, called metapeptone, soluble in excess of the acid, and which may be reprecipitated by concentrated mineral acids.

The following conditions favour or retard the transformation of albumen into peptones: it is accelerated by a temperature of 38° C., and by movement, and, on the other hand, it is retarded by fall and rise of temperature, being arrested at 5° and 60° C. It is also retarded by an excess of acid, alkali, or alcohol. The presence of an excess of peptones in the fluid also arrests the process.

The union of an acid and of pepsine, is indispensable in the digestive action of the gastric juice. It has been supposed that pepsine forms with the acid a combination, called *chloropeptic acid*, easily split up into its two components. This decomposition occurs principally in the presence of albuminates, and the hydrochloric acid set free dissolves and transforms the albuminates into peptones, while the pepsine thus liberated immediately recombines with a new quantity of hydrochloric acid to form chloropeptic acid, as before. This theory explains why it is that in addition to the presence of a fermentive substance, pepsine, a supply of free acid must also be available.

4. *General Conditions of Digestion.*—The conditions which affect digestion in the stomach are the following:

a. The secretion of gastric juice is incessant during the whole period of digestion in the stomach, and the food is mixed with the most suitable proportions of acid and of pepsine, and in the most convenient state of dilution.

b. The peptones are absorbed by the bloodvessels of the stomach along with other soluble matters and water as quickly as they are formed, or, they may pass with the rest of the food into the small intestine.

c. The movements of the stomach also facilitate the action of the gastric juice by bringing successively all parts of the food into close connection with the juice secreted by the mucous membrane.

Nervous Arrangements Connected with the Secretion of Gastric Juice.

During the intervals of digestion, the lining membrane of the stomach is of a pale greyish colour and is covered with a small amount of alkaline fluid, probably mucus. When excited mechanically by the entrance of food, or by a stimulating substance, such as a weak alkaline fluid, it becomes pink or even red in colour, and fluid is copiously poured from it. The secretion may also be excited by emotions or feelings, as on seeing or smelling or even remembering a savoury dish, a fact which indicates that it is somehow connected with the central nervous system. Rutherford has shown that when the pneumo-gastrics are cut during digestion the mucous membrane of the stomach becomes pale, and that stimulation of the peripheral end produced no effect while stimulation of the central end caused the membrane again to become red. These interesting facts would appear to show that impulses are transmitted from the stomach to the medulla along the pneumo-gastric which inhibit or restrain the action of a vaso-motor centre in that part of the nervous system. When this occurs, the nervous energy passing from it to the vessels of the stomach is weakened or removed, and consequently the vessels of the organ dilate. The motor tract by which influences pass to the vessels of the stomach so as to maintain them in a state of partial contraction is unknown, but, as from Rutherford's observation it cannot be in the pneumo-gastrics, it is probably in the sympathetic or splanchnic nerves. Any direct influence on gastric secretion, as is the case in the salivary glands, has not been discovered.

Results of Digestion in the Stomach.—By the combined influence of temperature, movement, and the physico-chemical action of the gastric juice, the food is reduced to a heterogeneous mass of matter having an acid odour and a colour and general appearance varying according to the nature of the food.

This matter is called *chyme*, and it consists of various salts; of water; of saccharine matter, which has been obtained from starch by the action of the saliva; of starch which has escaped the action of saliva, or has been set free by rupture of the walls of vegetable cells containing it; of fatty matter, either introduced as such in the food, or set free from animal cells; of albuminous substances of various kinds, either as peptones or in process of conversion into such; and of indigestible materials which are unsuitable for being acted upon by the digestive fluids. For practical purposes, it is necessary to study a little more in detail the specific effect of digestion upon albuminous proximate principles, and upon a few substances existing in almost every diet.

1. *Action on Proximate Principles.*

a. *Fibrine* swells, and in a short time is dissolved so as to form a clear fluid, which is not affected by heat.

b. *Fluid* or *Raw Albumen* is not coagulated, but assumes a milky appearance, probably from the connective tissue which it contains.

c. *Solid* or *Coagulated Albumen* becomes somewhat swollen, covered with flocculent matter, slowly disintegrates, and in course of time is reduced into a soft pulp, which may ultimately dissolve.

d. *Caseine* forms, after a considerable time, a turbid solution, which contains peptones of various kinds, including about 20 per cent. of dyspeptone, the presence of which may possibly explain the difficulty experienced by most persons in digesting such an article of diet as cheese.

e. *Gluten.*—Raw gluten disappears very quickly in the gastric juice, and it is said not to show the pulpy covering which is seen in semi-digested masses of other albuminous matters. When cooked, its digestion is exactly the same as that of coagulated albumen.

f. *Syntonine* is quickly converted into a coherent jelly, which is transformed into various kinds of peptones.

g. *Legumine* is quickly digested in gastric juice, and it has been asserted that this may occur with the action of acid alone, as legumine contains a substance analogous to pepsine.

h. *Gelatine* is dissolved rapidly in the gastric juice without being previously converted into a pulpy mass, and the solution, which may be called the peptone of gelatine, does not gelatinize in cooling, as a solution of ordinary gelatine would do.

i. *Gastric Juice* has no action upon elastic tissues, corneal tissue, cellulose, starch, and mucus, but it dissolves gum, cane sugar, and other soluble substances without affecting their composition.

j. *Salts* soluble in acidulated water, such as carbonates and phosphate of lime, may be dissolved, whilst carbonates may be transformed into chlorides with liberation of carbonic acid.

2. *Action on Certain Alimentary Substances.*

a. *Milk* is coagulated very rapidly in the gastric juice, the sugar and the salts dissolved in the fluid part are quickly absorbed; the fat, in the form of butter, is liberated by rupture of the walls of the milk globules;

and the caseine is converted by the gastric juice into peptone, as already described.

b. *Muscle.*—The fibres are separated with greater or less rapidity by solution of the connective tissue between them; the transverse striæ become well marked, and the fibres show a tendency to transverse cleavage. By these processes, the fibres are broken up into particles, which ultimately disappear. Digestion of muscle is more rapid when it is cooked, probably because that operation assists in breaking down the fibres.

c. *Connective Tissues.*—Such tissues as ligaments, tendons, membranes, and cartilages, especially if they be raw, are very slowly dissolved. When cooked, they are acted upon in the same manner as gelatine. Elastic tissue and nuclei are apparently unaffected by the digestive fluids. During digestion, fat is set free by solution of the cell walls.

d. *Vegetable Substances.*—In the raw condition, these are not easily digested by the human being, in consequence of their nutritive materials being usually enclosed in cellulose walls. When cooked, the walls of these cells are softened or ruptured so as to set free the sugar, starch, or gluten, contained in them, which are then acted upon in the manner already described.

Rapidity of the Digestive Process.—Numerous experiments made with artificial digestive fluids have shown that digestion goes on much more slowly in them than in the stomach. According to the experiments of Dr. Beaumont upon St. Martin's stomach, the rapidity of digestion varies according as the food is more minutely divided, whereby the extent of surface with which the gastric fluid can come in contact is proportionally increased. Liquid substances are for the most part absorbed by the vessels of the stomach at once, and any solid matters suspended in them, as in soup, are concentrated into a thicker material before the gastric juice operates upon them. Solid matters are affected so rapidly during health, that a full meal, consisting of animal and vegetable substances, may be converted into chyme in about an hour, and the stomach left empty in about two hours and a half. Dr. Beaumont found that among the substances most quickly digested were rice and tripe, both of which were digested in one hour. Eggs, salmon, trout, apples, and venison were digested in one hour and a half; tapioca, barley, milk, liver, and fish in two hours; turkey, lamb, and pork in two hours and a half. Beef, mutton, and fowls required from three to three and a half hours, and these were more digestible than veal. These facts were different from what was anticipated, and show that prevailing notions as to the digestibility of different kinds of food are very erroneous. It must be remembered, however, that easy digestibility does not imply high nutritive power. A substance may be nutritious, though so hard as not to be easily broken down; and many soft, easily digested materials may contain a comparatively small amount of nutriment.

General Hygienic Conditions. — Excluding individual peculiarities, these may be briefly stated as follows:—(1) The quantity of food taken — the stomach should be moderately filled, but not distended; (2) the time which elapsed since the last meal—this should always be long enough for the food of one meal to have completely left the stomach before more is introduced; (3) the amount of exercise previous and subsequent to a meal—gentle exercise being favourable, and over-exertion injurious to digestion; (4) the state of mind—tranquillity of temper being apparently essential to perfect digestion; (5) the bodily health; and (6) period of life—digestion being more active in the young than in the old.

Consult BEAUMONT, Exper. and Observations on the Gastric Juice, Boston, 1834.—An excellent popular account of digestion for non-professional readers will be found in COMBE'S Physiology of Digestion, edited by ARTHUR MITCHELL; consult, also, WUNDT'S Physiologie, p. 164; BEAUNIS' Physiologie, p. 384; LAUDER BRUNTON *ut supra*, p. 467; and FOSTER'S Text Book of Physiology, p. 175.

D.—CHANGES IN THE SMALL INTESTINE.

After the food has escaped from the stomach through the pyloric orifice, it is slowly propelled along the small intestine and mixed with three secretions, namely, the bile, the pancreatic juice, and the intestinal juice. It is therefore necessary to describe in the first place the movements of the intestine, afterwards, the physical and chemical characters of the juices, and finally the influence which these exert on the proximate constituents of food. It must be remembered also that as the chyme passes along the bowel, it is slowly losing water, soluble matter, and fats, as will be fully explained in treating of absorption.

1. MOVEMENTS OF THE SMALL INTESTINE.

These consist of regular and successive contractions from above downwards by which the calibre of the tube is diminished, and also of contractions in the direction of the long axis of the tube which appear to shorten the length of a small portion of it, and, when energetic, to move a loop of intestine as a whole. The circular contractions are no doubt due to the actions of the circular fibres, whilst the others depend on shortening of bundles of the longitudinal fibres. When carefully watched, in an animal recently dead, it is easy to observe that both sets of fibres in a segment of the bowel may act at the same time so as to produce a peculiar twisting movement which is unlike anything else. Such movements are termed *peristaltic,* and by them the food is slowly propelled along the intestine. It has been stated that there is a reverse current of more fluid matter in the centre of the bowel, but this is doubtful.

Nervous Arrangements of the Movements.—It is well known that there are two nervous plexuses in the coat of the intestine, the one (Meissner's plexus) found in the submucous coat of connective tissue, and the other (Auerbach's plexus) between the two muscular layers. The intestine is also supplied with filaments from the pneumo-gastric and splanchnic nerves. As peristaltic movements occur readily on stimulation after a portion of the bowel has been severed from its nervous connections, it is evident that these movements are regulated by ganglionic centres in the wall of the bowel itself. Peristaltic movements may be excited in a portion of intestine either mechanically or by electricity; and it has been found that the amount of blood supplied to the bowel has also an important influence upon them. Thus a state of emptiness or of great fulness of the vessels appears to excite the movements, and it has been supposed that the increased supply of blood to the bowel during digestion may act as a normal stimulus in carrying on the movement. The movement, however, may be influenced by the action of the pneumo-gastric or of the splanchnic nerves. Thus, stimulation of the pneumo-gastric increases, whilst stimulation of the splanchnic arrests, the movements. The pneumo-gastric may therefore be regarded as a motor nerve for reinforcing the activity of the ganglionic centres, and the splanchnic as an inhibitory nerve for restraining and controlling these centres. There can be no doubt also that intestinal movements may be influenced by impressions coming from the higher nervous centres, as is exemplified by the constipated condition which is frequently met with in nervous affections, and phenomena of a similar nature.

Consult regarding this matter WUNDT'S Physiologie, p. 152; LISTER: Proceedings of the Royal Society, 1858; and Report by PYE-SMITH and LAUDER BRUNTON, Trans. of the Brit. Association, 1875-76.

2. PHYSICAL AND CHEMICAL CHARACTERS OF THE JUICES.

The *bile* and *pancreatic juice* flow by a common orifice into the duodenum, about three or four inches below the pylorus, and the *intestinal juice*, secreted by Brunner's glands in the duodenum, and by the crypts of Lieberkühn throughout the whole length of the small intestine, mix with the chyme during its passage. The minute structure of all of these parts is fully given in Quain's Anatomy, Vol. II., pp. 357 to 380, and it is only within the scope of this work to describe the general characters of these secretions and the effects which they produce upon the chyme.

A. THE BILE.

1. *Physical and Chemical Characters of the Bile.*

This fluid, which is one of the products of the largest gland of the body, the liver, is to be regarded both as a digestive fluid and as an excretion. It will be convenient here, however, to give a short description of its general characters, to which reference may be again made when we discuss its history as an excretion.

For experimental purposes, bile may be obtained by the formation of an artificial fistula. This operation, which has been most frequently performed on dogs, is both difficult and dangerous. In the hands of competent observers, however, it has been the means of giving much direct information regarding the bile which could not otherwise be obtained, as biliary fistulæ in the human being are very rare.

Fresh bile is a yellowish-green fluid in herbivora, and it is reddish-yellow in man, and in most carnivora. It has a peculiar odour and a bitter taste. Specific gravity, 1026 to 1030; neutral reaction. After coming from the gall bladder, it contains a large quantity of mucus. When exposed to the air, it becomes more decidedly green in colour. A solution in concentrated sulphuric acid presents well marked fluorescence: it is pink by transmitted, and green by reflected light. In 1,000 parts, there are about 430 of solid matters, which consist of inorganic substances, cholestrine, colouring matters, and bile salts. In addition, the bile contains a considerable quantity of carbonic acid and traces of oxygen and nitrogen (see table, p. 44).

The *mineral matters* contained in bile consist of chlorides of sodium and of potassium, phosphates of soda, lime, and magnesia, carbonate of soda, oxide of iron, and traces of silica. In many cases, also, traces have been found of manganese and copper.

The *colouring matters* of bile are bilirubine and biliverdine, the general characters of which are described in appendix A. These matters, being insoluble in water, are kept in solution by the alkalies and bile salts. After bile has stood for sometime exposed to the air, other colouring matters are produced by oxidations of bilirubine.

The *bile salts* are glycocholate and taurocholate of soda. The glycocholate is found in small quantity in the bile of the human being, and of carnivora, whilst it is very abundant in that of herbivora. It may be obtained as a precipitate from an aqueous solution of crystallized bile, by the addition of dilute sulphuric acid. Taurocholic acid contains sulphur; it is found in the bile of carnivora, and in human bile is in much greater abundance than the other acid. In the fresh condition, bile does not contain any of the derivatives of these acids, but small quantities of other nitrogenous compounds, such as urea, lecithine, &c., may be found.

The following is an analysis of human bile in 1,000 parts:—[1]

Water,	862
Solids,	138
Salts of the bile acids,	82
Colouring matter,	22
Cholestrine,	26
Salts, consisting principally of chlorides of sodium and of potassium, and phosphates of soda, lime, and magnesia,	8

2. *Physiological Characters of the Bile.*

Quantity.—The quantity of bile secreted in 24 hours is much greater in herbivora than in carnivora; thus, while a dog will secret only $\frac{1}{50}$th of its weight, a rabbit will secret $\frac{1}{20}$th, and a guinea pig still more. Various estimates have been made as to the amount secreted by man, but the most probable is about $2\frac{1}{2}$ lbs.

Variations during Digestion.—Bile is secreted continuously and under a certain pressure, but the amount is increased during the different phases of digestion. In animals, such as the rabbit, in which the stomach is always more or less full, these variations are not so marked; but in man, and in the dog, the secretion increases shortly after the introduction of food, attains a maximum in from four to

---

[1] The variations produced in the composition of bile by the influence of the circulation and of the nerves will be stated in treating of biliary excretion.

eight hours thereafter, and then slowly declines. The total quantity of bile formed is also affected by the nature of the food. Thus it is greater after an aliment consisting of fat, and is smaller after a diet composed entirely of flesh. It is asserted that the quantity of bile is diminished by an insufficient diet.

3. *Action of the Bile on Elements of Chyme.*

The bile has no action upon albuminates, such as common albumen or fibrine, but it precipitates the peptones and parapeptones formed by the action of the gastric juice, and also the pepsine of this fluid. The precipitate thus formed is yellowish, flocculent, and resinous, and it adheres readily to the villi on the lining membrane of the bowel. Thus, the bile arrests the process of digestion of albuminates by the gastric juice,—as sometimes happens when, during what is called a bilious attack, it regurgitates into the stomach. The albuminates are, however, afterwards acted upon by the pancreatic and intestinal juices.

Bile has no direct action upon carbohydrates.

Bile is one of the principal agents in the digestion of fats. It dissolves a considerable amount of fatty acids, and it is believed that these unite with the alkaline bases of the bile salts, setting taurocholic and glycocholic acids free. The salts thus formed, and the bile acids then saponify any neutral fats in the intestine. (*Claude Bernard*). As the bile is an alkaline fluid, it also probably assists in the absorption of fats by lubricating the mucous membrane of the bowel. It may also act as a stimulant to the movements of the bowel, as a constipated condition usually exists when the bile is not poured in sufficient quantity into the alimentary canal. Finally, it may have an antiseptic action on the matters contained in the bowel.

B. The Pancreatic Juice.

1. *Physical and Chemical Characters of the Pancreatic Juice.*

The pancreas is a racemose gland, similar in structure to the salivary glands. The juice has been obtained from the dog and ox by fistulous openings.

When obtained pure, it is a limpid, colourless, slightly viscous fluid, which may form a thin coagulum on heating. Specific gravity, 1010 to 1015; strongly alkaline. It contains: (1) *albuminates* coagulable by heat; (2) *three ferments*, one of which transforms starch into sugar, the second decomposes the fats, and the third acts upon albuminous substances; (3) *nitrogenous bases*, such as leucine, guanine, tyrosine, xanthine, &c., are also found in small quantity; (4) *salts*, such as chloride of sodium, alkaline and earthy phosphates, and alkaline carbonates. The following is an analysis of 1,000 parts of pancreatic juice:—

	From a permanent fistula.	On opening the duct.
Water, ...	970·45	900·76
Solids, ...	29·55	99·24
Ferments, such as pancreatine, &c.,	22·71	90·44
Salts, ...	6·84	8·80
Soda, united to pancreatine,	3·32	0·52
Chloride of sodium, . .	2·50	7·35
Chloride of potassium, . .	0·93	0·20
Phosphate of lime, . .	0·07	0·41
Phosphate of soda, . .	0·01	...
Lime, united with pancreatine,	...	0·32
Magnesia.	0·01	...

2. *Physiological Characters of the Pancreatic Juice.*

Quantity.—From the dog about 4 grammes per kilogramme of the weight of the body have been collected in 24 hours. From these data, and taking into account the weight of the pancreas in man, it has been roughly calculated that from 200 to 250 grammes may be secreted by a human being in 24 hours.

Variations during Digestion.—The secretion of pancreatic juice is intermittent. It begins immediately after the introduction of food into the stomach, attains a maximum several hours afterwards, and then slowly diminishes. It is secreted, however, in very small quantities during the intervals of digestion. Judging from what has been seen in animals having a fistulous opening, at the commencement of digestion, it is viscous and very coagulable, and towards its close it becomes more limpid, is not coagulable, and has a much lower specific gravity. By such observations, also, it has been ascertained that a large amount of nutritious food increases not only the quantity, but improves the quality of the secretion, and that any circumstances affecting the general health of the animal have a contrary effect.

3. *Action of Pancreatic Juice on Elements of Chyme.*

The pancreatic juice has an influence upon starch, fats, and albuminoid substances: (1) By the action of a special ferment, which has been isolated, it transforms starch into sugar in a manner identical with the action of saliva, but much more rapid. It is asserted that the juice of the newly born child does not possess this property. (2) It has a double action upon fats: (*a*) forming an emulsion, in which the fatty particles are very finely divided; and (*b*) it decomposes the neutral fats into fatty acids and glycerine, and it has been supposed that the fatty acids thus set free unite with the alkalies of the pancreatic juice to form soaps. (3) The action of the juice on albuminous matter is more complicated, and may be divided into three successive stages, namely: (*a*) albuminates are converted into peptones, which are apparently identical with those formed by the gastric juice; (*b*) these peptones are partially converted into leucine and tyrosine; and (*c*) from the leucine and tyrosine thus formed, peculiar substances are produced, having a strongly fæcal odour, amongst which indol has been found. It is highly probable that in the normal state the greater quantity of the peptones thus formed are absorbed, and that the remainder are resolved into the derivative bodies just mentioned.

C. The Intestinal Juice.

1. *Physical and Chemical Characters of the Intestinal Juice.*

The juice, sometimes called the enteric juice, secreted by the glands of Brunner and the crypts of Lieberkühn, is very difficult to obtain in a perfectly pure condition. It is a transparent, limpid, slightly yellowish fluid, strongly alkaline, and coagulable by heat and by acids. Specific gravity, 1011. It contains about 2½ per cent. of solid matter, which consists of organic matter not yet identified, and salts, of which the chief is carbonate of soda. It also contains, according to Bernard, a ferment which transforms cane sugar into inverted sugar (a mixture of glucose and levulose). The mode of secretion of this juice, so far as variations during the digestive process are concerned, is unknown.

2. *Action of the Intestinal Juice on Elements of Chyme.*

From the difficulty of obtaining the juice in a perfectly pure condition, and free from admixture with the other digestive fluids, it has been found very difficult to ascertain its true functions. It appears to combine more or less all the properties of the other fluids, that is to say, it converts starch into sugar, emulsifies fats, and also acts upon albuminates.

RECAPITULATION.

It may be useful to the student briefly to recapitulate the chief facts relating to the changes which the chyme undergoes in the small intestine.

1. *General Characters of Intestinal Digestion.*

When the chyme passes through the pylorus into the small intestine, the action of the gastric juice is almost completely arrested, and the acid fluid excites the efflux of bile, pancreatic juice, and intestinal juice. As these juices are alkaline, they gradually neutralize the acidity of the chyme, so that that fluid towards the end of the duodenum becomes alkaline and remains so until the termination of the small intestine. In the small intestine, all the elements of food, albuminates, starches, fats, and sugars, are modified and transformed so as to be rendered assimilable. It is to be noted that the precipitation of peptones by the bile occurs only whilst the chyme is acid, so that the bile does not interfere with the digestion of peptones except in the upper part of the duodenum. In the upper part of the intestine, the chyme is coloured slightly yellow by the bile, but it becomes of a paler colour towards the lower end of the bowel. As it passes downwards, it gradually becomes more alkaline, and contains a smaller quantity of alimentary matters not digested, traces of leucine and tyrosine, and intestinal secretions, especially the bile. When it reaches the lower end of the bowel it has a fæcal character. The gases contained in the small intestine are nitrogen, carbonic acid, and hydrogen. The first two probably arise from the butyric fermentation of carbohydrates.

2. *Changes Produced in the Proximate Principles.*

These may be briefly stated as follows :—

1. *Starch* is converted into sugar by the action of the saliva, pancreatic juice, and intestinal juice.
2. *Cane Sugar* is converted into inverted sugar by the intestinal juice.
3. *Cellulose* may be converted into glucose. This is certainly the case in herbivora, but it is probable that in man most of the cellulose passes untouched.
4. *Fats* are liquefied in the stomach by the gastric juice dissolving the walls of the fat cells, and by heat. They are afterwards emulsified by the pancreatic juice, and slightly also by the bile. They are also split up by the pancreatic juice into glycerine and fatty acids, and these latter unite with the alkalies of the bile and of the pancreatic juice to form soluble soaps fit for absorption.
5. *Albuminates* are converted into peptones by the gastric, pancreatic, and intestinal juices. Some of the peptones formed by gastric digestion are precipitated by the bile in the duodenum, and are redissolved in the lower part of the intestine; and some of those formed by the action of the pancreatic juice are transformed into leucine and tyrosine.

6. *Gelatine* is simply dissolved by the digestive fluids, and it thereupon loses its power by gelatinizing. It is probably not converted into peptones.
7. All soluble *salts* are dissolved in the mouth and in the stomach by the saliva and gastric juice; the salts of lime and the phosphates of magnesia are dissolved by the gastric juice. Carbonates are decomposed, carbonic acid being set free, whilst the base unites with the hydrochloric or lactic acid of the juice. Organic salts, such as tartrates, malates, &c., are transformed into carbonates.
8. *Water*, and probably also alcohol, are directly absorbed.

3. *Résumé of the Action of the Digestive Fluids.*

The action of the digestive fluids may be thus briefly recapitulated:—

1. *Saliva*—converts starch into glucose, or grape sugar—converts cane sugar into inverted sugar.
2. *Gastric Juice*—converts albuminates into peptones—coagulates caseine of milk—dissolves albuminous walls of cells—disintegrates muscular fibre—dissolves gelatine.
3. *Bile*—precipitates part of the peptones—emulsifies fats—may decompose, and assists in absorption of, fats.
4. *Pancreatic Juice*—converts starch into sugar—converts cane sugar into inverted sugar—emulsifies fats—decomposes fats into fatty acids and glycerine—changes albuminates into peptones, and these into leucine and tyrosine, and the latter into indol and various fæcal substances.
5. *Intestinal Juice*—appears to combine, to a feeble extent, the properties of all the other juices.

E.—CHANGES IN THE GREAT INTESTINE.

When the alkaline chyme, poor in alimentary matters in consequence of absorption, reaches the great intestine, it has certain of the characters of fæces, and these become more marked towards the termination of the great intestine. This part of the alimentary canal receives only the secretion from numerous tubular glands, exactly similar to those of Lieberkühn in the small intestine. We shall consider (1) the movements by which the food is propelled onwards; and (2) the chemical and physical changes which occur in the bowel.

1. MOVEMENTS OF THE GREAT INTESTINE.

The movements of the great differ from those of the small intestine by occurring much more slowly, and, in consequence of the anatomical arrangements of the peritoneum, by permitting greater facility of moving one portion of the bowel with reference to another. In consequence of the slowness of the movements, the passage of material occupies a much longer time than in the small intestine, although the latter is at least three times the length of the great intestine. Thus the time occupied in the small intestine is from two to three hours, whilst from 12 to 24 hours are required for transmission through the great intestine. This arises from the matters remaining for a lengthened period in the cæcum, where they become more solid in consistence from the absorption of water. They are also delayed, probably, by the sharp ridges projecting into the interior of the bowel, which divide the elongated cavity into a series of loculi or compartments communicating with each other. Finally, the matters accumulate in the rectum, where they are retained by the action of the sphincters.

Nervous Arrangements of the Movements.—Nothing definite is known regarding this point, except that irritation of the pneumo-gastric excites the movements, whilst irritation of the splanchnic is followed by no effect. It is probable that the latter nerves may exercise an inhibitory influence over the ganglia in the wall of the bowel.

Movements of Defœcation.—Pressure of the fæces on the mucous membrane of the lower part of the rectum excites a desire, which is followed by evacuation. When this pressure does not pass a certain limit, the tenacity of the sphincter, to a certain extent under the control of the will, resists evacuation. When the desire reaches a certain intensity, there ensue a series of reflex intermittent contractions of the rectum, and of the sigmoid flexure of the colon, which tend to expel fæcal matters. These contractions overcome the resistance of the internal sphincter, but the external sphincter, by an effort of will, may be still firmly closed. If the desire be now yielded to, the matters are voided by the combined action of the rectum, and of the abdominal muscles, which latter are assisted in their efforts by fixation of the diaphragm. These muscles compress the abdominal cavity, and thus assist in expulsion. The movements are under the control of a special reflex centre, situated in the lumbar region of the spinal cord. It would appear, also, that this centre is under the control of still higher centres, as paralysis of the sphincters, and involuntary evacuations, occur when the higher centres are affected, as in coma.

2. PHYSICAL AND CHEMICAL CHANGES IN GREAT INTESTINE.

In consequence of fermentive changes, such as the liberation of fatty acids from fats, and the production of lactic acid from sugar, which occur in the small intestine, the matters in the great intestine exhibit an acid reaction. In man, alimentary matters do not undergo any further digestion in the great intestine, and the fæces are gradually formed from the refuse materials of food, biliary products, and various substances excreted from the wall of the bowel. In herbivorous animals, however, a kind of secondary digestion occurs in the greatly enlarged cæcum met with in these animals, and it is just possible that, to a very limited extent, the same process may occur in man. A portion of the bile reaches the great intestine, and is there transformed into taurine, glycocine, cholalic acid, choloidic acid, and dyslisine, all of which, along with bile acids and bile pigments, are found in the fæces.

Characters of the Fæces.—These have a peculiar odour, which is characteristic not only of the animal, but even of the individual, and varies from time to time. This odour is believed to depend upon the products obtained by the decomposition of peptones, and from excrementitious substances separated by the wall of the bowel. Fæces vary in colour, according to the kind of food and the amount of biliary matter present. Thus, with a rich animal diet, the fæces are dark coloured; with a vegetable diet, light, or slightly green; and a mixed regimen produces a brownish-yellow colour. They become clay coloured, and very offensive during jaundice, a condition in which little or no bile passes into the alimentary canal.

The microscopical examination of fæces shows the presence of elastic tissue, fragments of muscular tissue, cholestrine, fat globules, starch grains, epithelial cells, vegetable cells and fibres in various states of disintegration, and crystals of triple phosphate, &c.

The fæces contain 25 per cent. of solid matter, of which from 3 to 4 per cent. consists of various salts, the chief being the triple phosphate of ammonia and magnesia. A crystallizable body termed *excretine* has been obtained from fæces by Marcet.

The gases found in the great intestine consist of traces of oxygen, hydrogen, carbonic acid, nitrogen, light carburetted hydrogen, and sulphuretted hydrogen, and the quantity and kind of the gases would appear to depend upon the nature of the food. This is illustrated by the following table, which gives the composition of the fæces of a dog fed with animal and vegetable food (*Bischoff and Voit*) :—

	Flesh.	Fæces when fed with Flesh.	Bread.	Fæces when fed with Bread.
Carbon,	51·95	43·44	45·41	47·39
Hydrogen,	7·18	6·47	6·45	6·59
Nitrogen,	14·11	6·50	2·39	2·92
Oxygen,	21·37	13·58	41·63	36·08
Salts,	5·39	30·01	4·12	7·02
	100·00	100·00	100·00	100·00

Quantity of the Fæces.—Their quantity varies from 100 to 200 grammes per day, and it may even be so high in some individuals as 450 grammes. The amount is largely increased by a vegetable diet.

Having traced in detail all the processes by which the food is rendered fit for absorption during its passage through the alimentary canal, we now pass on to describe the mechanism by which the nutritious matter is taken up into the blood.

II.—ABSORPTION.

By absorption we mean the introduction of certain substances into the blood. These may enter the blood either directly through the walls of vessels, through an epithelial layer, or through the epidermis or uppermost layer of the skin. Thus we may have in the alimentary canal absorption by the capillaries of the mucous membrane, or by special vessels named lacteals; in the shut sacs of the body, such as the pleura and peritoneum, absorption may occur, in all probability directly into vessels connected with the lymphatic system; and the process is also carried on to a greater or less extent by the skin and pulmonary mucous membrane. It is important to note that by whatever channel matters may be introduced, their destination is the blood. For the sake of clearness, we shall first describe the physical and vital conditions of absorption in general, and afterwards consider the function as performed by special parts of the body.

1. General Conditions of Absorption.

These conditions depend on the nature of the absorbing surface, on the substances to be absorbed, upon the state of the blood, and upon the pressures to which both the absorbable matter and the blood are subjected. Thus, a very thin membrane, covered with squamous epithelium, as found in the pulmonary air-cells, will absorb readily, whilst with a thick layer of cells, such as exists in the epidermis of the skin, absorption will be slow, or almost impossible. Substances having a large endosmotic equivalent, as the colloids, are absorbed with difficulty, except under certain circumstances. For example, albumen passes through membranes more readily when it is united with an alkali.

Concentration of a solution also favours absorption. Absorption is also affected by the quantity and the quality of the blood. The process goes on with rapidity when a large quantity of blood passes along the absorbing surface in a unit of time, as in mucous membranes richly supplied with capillaries. Increase of blood pressure, on the other hand, diminishes absorption, whilst increase of pressure on the other side of the absorbent membrane will probably favour it. Finally, it would appear that substances which already exist in the blood in considerable quantity are difficult of absorption, so that the quality of the blood also affects the process. Absorption, no doubt, depends to a great extent on osmosis, in various circumstances, and the practical difficulty is to determine what the conditions in the living body really are.

2. Intestinal Absorption.

Matters are taken up from the intestinal canal by capillaries, and by special vessels which belong to the lymphatic system. It is difficult to determine experimentally the part which the two orders of vessels fulfil in absorption, by reason of their intimate anatomical connection. Attempts have been made to ligature either the bloodvessels or the lymphatics coming from a portion of the bowel, and to study the results, but it is evident that difficulties arise, due to anatomical arrangement, which are so great, and involve so many sources of fallacy, as to make uncertain any conclusions drawn from such experiments. The general results, however, may be briefly stated :—

1. *Absorption by the Capillaries.*—The mucous membrane of the stomach and small intestine, in which organs absorption occurs, is richly supplied with capillary bloodvessels placed immediately beneath the epithelial layer. In in-

jected preparations, the capillary plexus is so distinctive in character as to identify at once the mucous membrane to which it belongs. Thus, in injections of the stomach, the capillaries form a series of meshes of irregular shape; in the small intestine, the vessels exist as a net-work, from which arise numerous loops, passing into the villi; whilst, in the great intestine, the mesh-work is so regular as to present the general appearance of a honey-comb. All of these vessels during life are filled with blood, moving onwards as a current, of a certain specific gravity, and exerting a certain amount of pressure on their inner surface. On the other side, and separated by the walls of the vessels, by some connective tissue, and by an epithelial layer, we find the chyme, containing many crystalline and fluid substances. It is evident that, under these circumstances, the conditions are favourable for the passage of a certain amount of material directly into the blood. It is to be noted, also, that from the anatomical arrangements of the portal system, the whole of the matters thus absorbed must pass to the liver. So far as can be ascertained, the matters absorbed by the capillaries are peptones, sugar, water, and salts. It is manifestly difficult to determine what changes *peptones* may possibly undergo during the process of absorption; but it is evident that they must undergo some change, as the quantity of bodies analogous to peptones which have been found in the blood does not correspond to the amount of peptones absorbed from the alimentary canal. Their endosmotic equivalent is very small. The absorption of peptones occurs, in the first instance, in the stomach, and is afterwards continued throughout the whole length of the small intestine, and probably also in the cæcal part of the great intestine.

There can be no doubt that *sugar* passes directly into the capillaries, but it has not yet been proved that it contributes in any way to the formation of glycogen. Neutral *fats* do not pass directly into the blood; but it is quite possible that they may do so in the form of soaps. Whatever may be its explanation, it is a fact that the capillaries and small blood-vessels of the alimentary tract frequently contain fat. Water, soluble salts, alcohol, &c., are absorbed directly by the vessels.

2. *Absorption by the Villi.*—The villi are small conical appendages of the mucous membrane of the small intestine which contain in their interior a delicate cæcal tube, called the commencement of a *lacteal* vessel. The general arrangement of the villi, and a diagrammatic view of the structure of a villus are seen in Figs. 47 and 48. The lacteals from contiguous villi unite to form a plexus of vessels in the wall of the bowel, which terminates in one or more larger vessels.

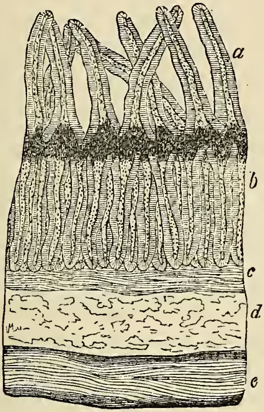


Fig. 47.—Vertical and Longitudinal Section of the small Intestine in lower part of the Jejunum, shewing the general arrangement of its coats: *a*, villi; *b*, intestinal tubes or follicles of Lieberkühn; *c*, submucous areolar tissue; *d*, circular muscular fibres; *e*, longitudinal muscular fibres.

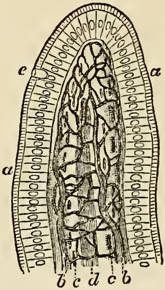


Fig. 48.—Diagrammatic View of the upper part of a *Villus;* *a a*, columnar epithelium; *e*, *goblet cell;* *b b*, artery and vein; *c*, nuclei of connective tissue; *d*, commencement of lacteal.

The latter carry the fluid absorbed to glands in the mesentery, and from thence it passes to still larger vessels, terminating in the *receptaculum chyli*, which may be regarded as a general reservoir for all parts of the intestinal absorbent surface. The nutritive matter in this system of vessels now receives the name of *chyle*, and the vessels themselves, from the milk-like appearance of the fluid in them, are termed *lacteals*. The outer surface of a villus is covered by columnar epithelium, in the cells of which some observers have stated that they have seen vertical striæ, indicating, in their opinion, delicate canals, along which nutritive matters might pass to the lacteal. (A description of the structure of the villi will be found in Quain's Anatomy, vol. ii., p. 360). In addition to the lacteal, it must be remembered that each villus contains a plexus of capillaries, which may absorb water and soluble matters in the same manner as the capillaries of other parts of the alimentary tract, and that each also contains one or more involuntary contractile fibre cells. It is generally believed that the special function of the lacteals is the absorption of fat. After the digestion of a meal containing fatty matter, the epithelial cells covering the villi contain highly refractive particles of fat, and these are also found between the epithelial basement membrane and the commencement of the lacteal. The exact arrangements by which this is effected are still unknown. Along with fat, water and various salts are also absorbed. In treating of the circulation of lymph, a fluid which presents certain analogies to the fluid found in the lacteals called *chyle*, a description of the mechanism by which the chyle is propelled onwards will be given.

3. *Chyle.*—During digestion, more especially if the food contain a considerable quantity of fatty matter, the lymphatic vessels of the mesentery, commonly called *lacteals*, are filled with a milky fluid, the chyle. It is a feebly

alkaline, milky or opalescent liquid, having a specific gravity of 1020. When examined under the microscope, it is found to consist of a fluid, in which are three histological elements, namely, numerous molecules, constituting what has been called the molecular basis of the chyle; (2) highly refractive particles of fat or oil; and (3) certain cells, of irregularly globular form containing numerous minute granules, and similar in all respects to those known as the colourless corpuscles of the blood. Prior to the passage of the chyle through the mesenteric glands, it abounds chiefly in molecules and fatty particles, but afterwards these are less numerous, and the cells above described make their appearance.

FIG. 49.—Drop of Chyle. On the left, corpuscles lying amongst molecular matter; on the right, corpuscles altered by the addition of acetic acid.

When chyle is removed in quantity from the *receptaculum chyli*, or from the thoracic duct, it forms a coagulum of feeble consistence, but it would appear that this property does not exist in the chyle before it passes through the mesenteric glands.

The following is an analysis showing the percentage composition of chyle taken from the thoracic duct of a decapitated criminal:—

Water,	90·48
Albumen and fibrine,	7·08
Watery extracts,	0·56
Alcoholic extracts,	0·52
Fats,[1]	0·92
Salts,	0·44

The *quantity* of chyle formed per day cannot be estimated with accuracy. On the supposition that the whole of the fat introduced into the food is taken up into the chyle, it

---

[1] Analysis of the chyle of the ox has shown usually nearly 3 per cent. of fats.

has been estimated that 3 kilogrammes are formed per day. (*Vierordt*).

3. CUTANEOUS ABSORPTION.

The skin may absorb in certain conditions matter either in the form of a gas, a liquid, or a semi-solid substance. The absorption of gases and of volatile matters by the skin has been long known. Thus, an animal may be poisoned by plunging its body in an atmosphere of sulphuretted hydrogen, after every precaution has been taken to prevent the entrance of the gas into the respiratory passages. Much controversy has taken place as to the possibility of absorption of liquids by the skin. The layer of sebaceous or oily matter which covers its surface, and the thick stratum of more or less modified epithelial cells forming the epidermis would appear almost to render absorption impossible. On the other hand, experiment has shown that a small quantity of water and soluble substances may pass into the blood through the skin during immersion in baths, and that even oily matters may be absorbed with the aid of friction. It is well known, also, that the repeated external application of mercurial ointment to the skin may be followed by the physiological effects of that substance. In these cases, absorption probably occurs by the matters penetrating the ducts of the sebaceous and sudoriparous glands.

4. PULMONARY ABSORPTION.

Gases and volatile substances are absorbed with great rapidity through the lining membrane of the pulmonary passages. Although fluids and soluble substances are absorbed more slowly, it is remarkable that a large portion may quickly be taken up. Thus, the entrance of water into the air-passages of an animal, up to a certain limit, is not followed by asphyxia. It is very difficult to account for the presence of particles of carbon or of silica in the bronchial glands, and tissues of the lungs, of persons employed in certain occupations.

5. ABSORPTION BY SEROUS MEMBRANES.

In the course of inflammatory affections, serous fluids frequently accumulate in the shut sacs of the body, such as the pleura or the peritoneum, and these fluids may, after a time, become absorbed. Histological research carried on by numerous observers, and in particular by Recklinghausen and Klein, has shown that in serous membranes, lined by a single layer of endothelial cells, numerous openings, termed *stomata*, occur, which communicate with the lymphatic system. In all probability, absorption may take place both by these channels and by the bloodvessels.

6. ABSORPTION IN CONNECTIVE TISSUE.

When a soluble substance is introduced into the cellular tissue underneath the skin, it is absorbed with great rapidity, a fact which has been taken advantage of in the method of the subcutaneous injection of remedies, first practised by Alexander Wood of Edinburgh.

7. ABSORPTION IN TISSUES AND THE FORMATION OF LYMPH.

As has been already pointed out, the tissues are nourished by fluid matter which exudes through the walls of the capillaries. A portion of this fluid matter is probably at once taken up by, and incorporated with, the living protoplasm of the tissues; and the remainder, which may be regarded as being in excess, must be removed, because probably chemical changes occurring in it would produce substances injurious to the tissues. It is also to be remembered that one of the conditions of the activity of living tissue is chemical decomposition of some of the materials of the tissue; the living matter dies, undergoes molecular changes, and now, regarded as a waste product, finally passes again into the fluid state, so that it may be readily removed. The exact mechanism by which the excess of nutritious matter and the waste products are removed is still obscure, and it is difficult to say to what extent reabsorption into the blood may occur, or whether such matters must be carried away by a special set of vessels—the lymphatics.

In recent times, the researches of histologists have thrown a flood of light on the relation that exists between the origin of the lymphatics and the elementary tissues. It has been shown that lymphatics abound in nearly all the textures and organs which receive blood, and in many cases a lymphatic vessel may completely or partially surround an artery or a vein. Lymphatics either originate in a *plexus*, from which a larger vessel carries the lymph towards the lymphatic duct, or in *lacunæ*, or spaces lined by flattened epithelium cells, which exist in many organs, more especially in glands. These "interstitial receptacles," connected by lymphatic vessels, present a remarkable analogy to the vascular system of insects and crustacea, and it is not improbable that it is homologous with it. It is also physiologically important to note that the masses of protoplasm, called connective tissue corpuscles, which abound in many tissues, lie in spaces which communicate freely with each other, the passages joining them being frequently tubular in form, so as to constitute a series of small pores or canals. Thus there appears to be, more or less, through-

Fig. 50.—*a*, *b*, *c*, *d*, Various forms of connective tissue corpuscles.

out every tissue, what may be termed a drainage system for the purpose of carrying off waste products and excess of pabulum, as the *lymph.* But the lymph—and the same is true of the chyle—so far as we know at present, does not pass directly into the blood. It is conveyed in the first instance to *lymphatic glands,* small solid bodies placed in the course of the lymphatics and lacteals, the structure of which is very remarkable.

A lymphatic gland is covered externally by a sheath of connective tissue, from which partitions pass inwards, so as to divide the cortical part of the gland into a series of compartments. Both the sheath and the partitions frequently contain involuntary muscular fibre. In the compartments, called *alveoli,* thus formed, we find a *pulp* made up of densely crowded lymph corpuscles lying in a fine meshwork of retiform tissue. The medullary, or central part of the gland consists of rounded cords forming a network, in the spaces of which the same kind of pulp is found. Both in the cortical and in the medullary part, spaces exist around

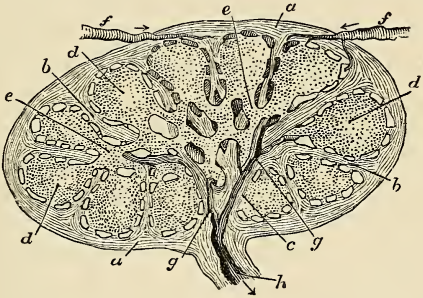


FIG. 51.—Section of a Lymphatic Gland; *a, a,* strong fibrous capsule sending partitions into the gland; *b,* partitions between the follicles or pouches of the *cortical* or outer portion; *c,* partitions of the *medullary* or central portion; *d, e,* masses of protoplasmic matter in the pouches of the gland; *f, f,* lymphvessels which bring lymph *to* the gland; *g,* confluence of those leading to the efferent vessel, *h,* which carries the lymph away *from* the gland.

the pulp, which have been termed the *lymph channels.* A lymph channel, however, is not a free space, as it is also occupied here and there by very delicate retiform tissue; and, during life, it is filled with lymph containing numerous cells. It has also been ascertained that the vessels carrying the lymph to the gland, *afferent vessels*, end in minute branches opening into the alveoli of the cortical portion, whilst those which carry lymph from the gland, *efferent vessels*, originate in a plexus in the medullary portion It is important to notice this anatomical distribution. Lymphatic glands are also richly supplied with bloodvessels which form a capillary network, so that the blood must be brought into close relation with the elements of the lymph.

We have at present no accurate knowledge of the changes which occur in a lymphatic gland, but in all probability they are of the following nature: (1) Exchanges as regards fluids, gases, and soluble substances between the blood and the lymph, which will be favoured by the comparatively slow movement of the latter fluid; and (2) The continual production of new protoplasmic elements, in the form of lymph corpuscles, probably by fissiparous division. That the latter phenomenon occurs is supported by the fact of these corpuscles existing in greater quantity in lymph after it has passed through a gland. It is difficult to say whether the pabulum which enables the protoplasm to multiply in this manner is obtained from the blood or from the lymph. After passing through lymphatic glands, the lymph reaches the venous system by the thoracic duct and by the right lymphatic duct, both of which open into great veins at the root of the neck.

Consult regarding the structure of the lymphatic system—QUAIN, Vol. II., pp. 183–200; also KLEIN on the Anatomy of the Lymphatic System, the Lung, and the Serous Membranes.

1. *Physical and Chemical Characters of Lymph.*—When obtained tolerably pure from the thoracic duct, it is a colourless, or slightly opalescent fluid, feebly alkaline, and having a specific gravity of 1045. It contains numerous corpuscles precisely similar to the colourless corpuscles of the blood, and sometimes a few coloured corpuscles. Unlike the chyle, only a very small quantity of molecular matter is found in it. It forms a soft coagulum, thus separating into a clot and a fluid. The fluid, or serum, contains 3 per cent. of albuminous matters, a small quantity of leucine, urea, &c., fats, fatty acids, volatile fatty acids, especially butyric acid, cholestrine, and various salts, such as the phosphates of potash and soda, chloride of sodium, sulphates, and traces of iron. In chemical composition, it shows a close approximation to chyle, except that in the latter albumen and fats are in greater quantity, as may be seen by the following table showing the analysis of the lymph and chyle of an ox, made by Wurtz:

	Lymph.	Chyle.
Water,	938·97	929·71
Fibrine,	2·05	1·96
Albumen,	50·90	59·64
Fats,	0·42	2·55
Salts,	7·63	6·12

2. *Quantity of Lymph.*—It has been estimated that an amount of lymph is formed in 24 hours equal to about $\frac{1}{12}$th of the weight of the body. Colin, a distinguished comparative physiologist, obtained from a horse 42 kilogrammes in 24 hours, or 105 grammes for each kilogramme of the animal's weight.

3. *Movements of the Chyle and Lymph.*—Both the chyle and lymph move from the radicles of the vessels towards their trunks. The movement is slow, as compared with that of the blood. Numerous researches indicate that the efficient

cause of this movement in the higher animals is the pressure of the blood in the arteries. Thus, increase of pressure is followed by an increased discharge from severed lymphatics, and, no doubt, this pressure operates, to a certain extent, at the radicles of the vessels. But there are other accessory agents, such as the presence of valves so arranged that compression, by muscular action, must force the lymph and chyle onwards, and also the movements of respiration,—inspiration accelerating the movements in the lymphatic duct, whilst expiration diminishes it. In addition, the contractions of the involuntary muscular fibres found in the lymphatic glands and lymphatic vessels must assist in propelling the fluid. Rythmical contractions of the lymphatics of the mesentery have been actually observed, and it is well known that special contractile sacs, sometimes called *lymph-hearts*, are met with in many animals, such as the frog. The pressure of the lymph in the vessels has been ascertained by Weiss to be about 11 millimetres of mercury, and the same observer noted that it travelled at the rate of 4 millimetres per second. The movements of the chyle may depend partly on the pressure to which the fluid in the intestine is subjected, and partly to the action of the muscular fibres in the villi.

III.—THE BLOOD.

This fluid contains all the elements necessary for the nutrition of every part of the body, and it is essential to study its history with the greatest care. We shall therefore consider: (1) the mode of its formation; (2) its physical, morphological, and chemical characters; (3) the changes which it undergoes when removed from the body; and (4) the mechanism by which it is circulated.

A.—FORMATION OF BLOOD.

As has been already explained, the blood is frequently receiving new materials from the alimentary canal and from the lymphatic system. From the first, it receives matters either directly by the bloodvessels or indirectly by the chyle; and from the second it receives lymph. In addition, a small quantity of matter may be absorbed by the skin, or by serous membranes. Oxygen, and possibly a small quantity of volatile matters, are also introduced by the respiratory tract. Finally, the blood receives protoplasmic elements from, and probably its fluid parts are elaborated by, certain glands throughout the body, frequently called blood-glands.

THE BLOOD-GLANDS.

These consist of the lymphatic glands generally, of the glands of Peyer, of the spleen, supra-renal capsules, thyroid and thymus glands, and of the pituitary and pineal glands. The structure of these bodies is described in anatomical and histological works, and all that will be attempted here is to indicate certain general features which are of physiological importance.

1. *The Glands of Peyer.*—These may be considered as the first series of lymphatic glands. They are scattered over the intestinal mucous membrane from the stomach (*Allen Thomson*) to the rectum, and may be solitary or aggregated together in patches; the latter become larger as they descend the small intestine. They consist of a shut sac composed of fibrous tissue, lined by a layer of epithelium, and they contain protoplasmic matter, which appears in preparations as molecules and nuclei, and they also contain a few cells, similar to the colourless corpuscles of the blood, which may be called *lymphatic elements.*

2. *The Spleen.*—This organ is composed of a fibrous envelope which sends in bands or trabeculæ uniting with one another, so as to divide its substance into irregularly-sized spaces filled with a reddish pulp. The pulp consists of protoplasmic matter, and cells, mingled with blood corpuscles isolated or grouped together—often surrounded by an albuminous envelope—in all stages of disintegration. The trabeculæ contain numerous nucleated fusiform cells. It is richly supplied with lymphatics and bloodvessels. Connected to the coats of the smaller arteries are shut sacs, from the $\frac{1}{30}$th to the $\frac{1}{60}$th of an inch in diameter, resembling, in general structure, the glands of Peyer, called the Malpighian *bodies of the spleen*, containing lymphatic elements.[1]

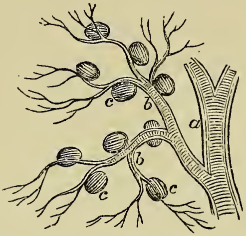


FIG. 52.—Portion of Splenic Artery, *a*, *b*, *b*, having Malpighian bodies attached, *c*, *c*, *c*.

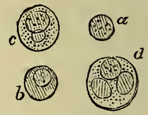


FIG. 53.—Cells from the Spleen Pulp: *a*, similar to a colourless corp uscle of blood; *b*, nucleated cell; *c*, bi-nucleated cell; *d*, cell containing three cells in interior.

3. *The Supra-renal Capsules* consist of a cortical and medullary portion: the former is composed of elongated shut sacs varying in size, lying side by side, which contain the same lymphatic elements as the glands of Peyer and the Malpighian bodies of the spleen. The medullary portion is essentially fibrous, with granular cells embedded in its substance.

---

[1] These must be carefully distinguished from the bodies in the kidney, also associated with the name of Malpighi, which have an entirely different structure.

Addison considered that disease of these organs produced a dark brown or sallow tint in the skin, and there can be no doubt that the two often coincide, and constitute what is known as *Addison's disease.* But the exceptions are so numerous as to prevent our belief in a necessary connection between one and the other.

4. *The Thymus Gland* consists of hollow lobules or pouches united together by fibrous tissue, and filled with the same lymphatic tissue as exists in the other blood-glands. The pouches communicate with a central reservoir from which there is no outlet. The gland is large in the human infant shortly after birth, but in a few years it commences to diminish in size, and after puberty its place is occupied chiefly by a mass of fat. Hence it is only active as a blood-gland during early childhood, and loses its glandular character as age advances.

5. *The Thyroid Gland* consists of a dense fibrous stroma, embedded in which are numerous shut sacs, filled with the same lymphatic elements that have been referred to, and lined by an epithelial membrane. It also, like the thymus, is comparatively larger in infancy, but in adult age it does not degenerate so much as the thymus by fatty changes, as by the deposition into the shut sacs of colloid or glue-like matter. A permanent enlargement of this gland is termed *goitre,* an affection not unfrequently associated with a peculiar kind of mental imbecility, called *cretinism.*

6. *The Pituitary and Pineal Glands,* in their general structure, resemble the glands just noticed, being composed of fibrous tissue enclosing shut sacs, the latter containing calcareous deposits. This renders it probable that at an early period of life they performed similar functions to the blood-glands.

All these organs resemble one another in structure, consisting of pouches or shut sacs, rich in protoplasm, and containing many nuclei. They have no ducts, are very vascular, and the lymphatics passing from them terminate in the thoracic duct. No difference whatever can be distinguished between the contents of these organs and those of the lymphatic glands; and other facts connected with their morbid states—more especially the production of *leucocythæmia*[1]—serve to convince us that, like them, they are connected with sanguification, hence their modern name of blood-glands. The whole system of lymphatic glands may be said to secrete or form certain elements of the blood. Hewson was the first to suppose that they formed the blood corpuscles. Like ordinary lymphatic glands, they certainly produce numerous masses of protoplasm in the form of colourless blood corpuscles, but their share, if they have any, in the formation of the coloured corpuscle is still unknown. In addition to these glands, the marrow of bones appears to have some relation to the formation of blood, as it contains numerous cells exactly similar to the colourless corpuscles. As to the origin and end of the coloured corpuscles, we are still in ignorance, nor can we trace precisely their relation to the colourless cells. Attempts have been made to show that they are probably the free nuclei of colourless cells, a supposition which has a few dubious facts to rest on, and which is not very

---

[1] A remarkable disease, characterized by anæmia, debility, and the existence of an excessive amount of colourless corpuscles of the blood. There can be no doubt that the opinions of Hewson, applied by Virchow to the explanation of this disease, namely, that these glands have to do with the formation of blood, exercised a most important influence on our present theories as to the formation of blood. The whole subject, however, is still in obscurity. It is to be noted that the disease was identified and described almost simultaneously by Hughes Bennett and Virchow, and that the latter was the first to state its true pathology.

probable. In these glands, also, exchanges no doubt take place between the blood and the lymph.

Consult, as to the functions of the blood-glands, the works of Hewson, published by the Sydenham Society; Virchow's Cellular Pathology, translated by Chance; and Bennett's work,—Leucocythæmia, or white-cell blood, in relation to the physiology and pathology of the lymphatic glandular system.

Thus, to recapitulate, it appears that the blood is frequently receiving new supplies of material from the following sources :—

1. Water, salts, sugar, peptones, &c., by vascular absorption from the alimentary canal.
2. Water, salts, peptones, fats, either free or as soaps, &c., by lacteal absorption from the alimentary canal.
3. Water, and possibly some volatile or soluble matters by the skin.
4. Oxygen, and possibly some aqueous vapour and volatile matters by the mucous membrane of the lungs.
5. Water, salts, nitrogenous matters, &c., from the lymph or from shut sacs into which fluids had been previously effused.
6. Protoplasmic elements from the lymphatic glands, mesenteric glands, and other blood-glands, in which also no doubt exchanges occur between the chyle or lymph and the blood. From these protoplasmic elements, the coloured corpuscles may possibly be formed.

B.—PHYSICAL, MORPHOLOGICAL, AND CHEMICAL CHARACTERS OF BLOOD.

1. Physical Characters of Blood.

The blood, whilst in the vessels, is a fluid of a red colour, which may vary from a crimson, as seen in arteries, to a reddish purple, as in veins. A thin stratum spread on the surface of a sheet of glass is opaque, but the addition of water or chloroform, or the application of extreme cold, or of a temperature above 60° C., or the continuous action of electricity, causes such a layer to become translucent. When a drop is examined by transmitted light on the stage of the microscope, it is found to consist of an almost colourless fluid in which there are numerous corpuscles of a straw-yellow colour, and a few corpuscles of a larger size, which present no colour. Blood has usually an odour peculiar to each species of animal (*halitus sanguinis*). Soon after blood has been removed from the body, it separates into two parts, a clot and a fluid, a process which is known as the *coagulation of the blood,* and which will be afterwards described.

2. Morphological Characters of Blood.

If we examine a drop of human blood with a magnifying power of 300 diameters, two kinds of corpuscles may be observed:—(1) The *red,* or *coloured;* and (2) the *white,* or *colourless.* The coloured, which are readily distinguished by their yellow colour, sharp, well-defined outline, and the shaded appearance in the centre—indicating that they are bi-concave discs—usually adhere together by their flat surfaces, thus forming rouleaux, like piles of coins. These rouleaux cross each other so as to make a mesh-work, in the spaces of which, here and there, a colourless corpuscle may be readily identified by its want of colour, larger size, somewhat irregular form, and granular aspect.

1. *The Coloured or Red Corpuscles.*—In man, and in all mammals with the exception of the *Camelidæ,* the form of the coloured blood corpuscles is that of a bi-concave, non-nucleated, circular disc. In the camelidæ, they are oval and biconvex. In birds, reptiles, and fishes, the corpuscles are oval, biconvex, and nucleated. Study Figs. 54 and 55. No

corpuscles similar to the coloured corpuscle is found in the blood of invertebrates, where, however, bodies not unlike the colourless corpuscles are met with.

The size of these corpuscles varies greatly in different animals. The most careful and elaborate researches on this subject have been made by Gulliver, who has given the following measurements in fractions of an inch :—

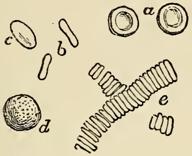


FIG. 54.—Blood-corpuscles; *a*, two coloured corpuscles shewing shadowed appearance in the centre, indicating biconcave form; *b*, corpuscle seen edgeways; *c*, slightly oval corpuscle; *d*, colourless corpuscle; *e*, coloured corpuscles in rouleaux.

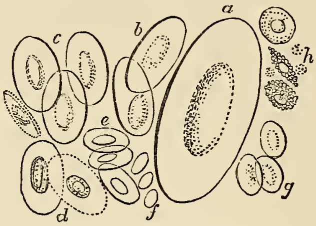


FIG. 55.—Blood-corpuscles of various animals magnified in the same scale: *a*, from proteus; *b*, salamander; *c*, frog; *d*, after addition of acetic acid, showing nucleus; *e*, bird; *f*, camel; *g*, fish; *h*, crab or other invertebrate animal.

	Diameter.
Man,	$\frac{1}{3200}$
Elephant,	$\frac{1}{2745}$
Musk Deer,	$\frac{1}{6300}$

	Long Diameter.	Short Diameter.
Camel,	$\frac{1}{3250}$	$\frac{1}{5921}$
Ostrich,	$\frac{1}{1649}$	$\frac{1}{3000}$
Pigeon,	$\frac{1}{2314}$	$\frac{1}{3429}$
Humming Bird,	$\frac{1}{2666}$	$\frac{1}{4000}$
Frog,	$\frac{1}{1108}$	$\frac{1}{1821}$
Crocodile,	$\frac{1}{1231}$	$\frac{1}{2286}$
Proteus,	$\frac{1}{400}$	$\frac{1}{727}$
Pike,	$\frac{1}{2000}$	$\frac{1}{3555}$
Shark,	$\frac{1}{1143}$	$\frac{1}{1684}$
Earth-worm,	$\frac{1}{110}$	$\frac{1}{1200}$
Leech (after addition of water),	$\frac{1}{3000}$	$\frac{1}{3600}$

The size of the coloured corpuscles bears a relation to the calibre of the ultimate capillary vessels, which are just large enough to admit of their passage in single file. Injections, therefore, of the bloodvessels are more easily made in reptiles than in any other animals.

The addition of water causes the coloured corpuscles to lose their colour, to swell out, and become globular. Syrup, gum, albumin, and dense saline solutions, render them flaccid, mis-shapen, irregular in outline, contracted, puckered, &c. Acetic acid appears at first wholly to dissolve mammalian corpuscles, but their form may be faintly recognised on adding to them tincture of iodine. But on the oval corpuscles of birds, reptiles, and fishes, the effect is simply to dissolve, or render very transparent the cell wall, whilst the nucleus is unaffected, and rendered more clearly visible in the field of the microscope. Astringent solutions, and especially a solution of nitrate of silver, cause puckerings and folds to appear in the cell wall. This is well seen in the corpuscles of the newt, where also a solution of boracic acid develops the nucleus in the form of an oval body, from which processes radiate outwards. A solution of magenta causes a minute molecule to appear on the external margin, as pointed out by Dr. Roberts of Manchester. The same observer, also, was the first to describe the effect of a dilute solution of tannic acid, which causes one, and sometimes two, protrusions to take place from the corpuscle. A stream of carbonic acid passed into frog's blood, is quickly followed by the appearance of the oval nucleus, which may again disappear under the action of air, or of oxygen.

Various estimates have been made of the number of red corpuscles, the mean of which is that five millions are contained in the space of a cubic millimetre, that is, in the space occupied by a very small drop; and Welcker has calculated that if the coloured corpuscles of the adult human being were placed side by side on a flat surface, they would cover an area of 2816 square metres, or about 3000 square yards. They thus present a widely extended surface for the oxidation processes in which they are engaged. It has also been ascertained that in healthy blood there are from 400 to 500 coloured to each colourless corpuscule.[1]

2. *The Colourless* or *White Corpuscles.*—These bodies, sometimes called *leucocytes*, are colourless, irregularly spherical, and larger than the coloured corpuscle, being about the $\frac{1}{2000}$ to $\frac{1}{2500}$ of an inch diameter. When examined with high powers, say 800 diameters, they are seen to be masses of protoplasm containing a few granules.

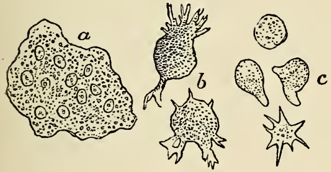


Fig. 56—*a*, mass of nucleated protoplasm from marrow of bone; *b*, lymph-cells, from inflamed eye, showing amæboid processes; *c*, various forms of colourless cells of the blood.

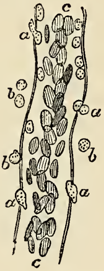


Fig. 57—Bloodvessel in mesentery of frog during inflammation, showing migration of colourless cells of the blood: *a*, cells passing through membranous wall of vessel; *b*, cells which have passed through; *c*, coloured cells in stream of blood.

The most remarkable characteristic of these corpuscles is their power of performing amæboid movements. When watched attentively they may be observed assuming slowly various forms, such as are represented in Fig. 56. These

---

[1] An estimate may now be made with tolerable ease by the ingenious method of Malassez, which will be described in the Lessons on Practical Physiology.

movements occur more readily with a temperature the same as that of the body. By such changes of form, also, they may wander from place to place, and even pass through the walls of bloodvessels, as depicted in Fig. 57, a phenomenon which is now regarded as one of the most important in the inflammatory process.

3. *The Structure of Blood-clot.*—When a recent blood-clot is examined microscopically, it is found to consist of a network of extremely delicate fibres of fibrin, enclosing blood corpuscles in the meshes; and if the upper part of the clot be the part inspected, the colourless corpuscles are numerous, whereas in other parts they occur, relatively to the white, in about the same proportions as in blood. There can be no doubt that, by the development of vessels from the sides of the cavity in which it is placed, and possibly from changes in the colourless corpuscles, the clot may become firm and organized into a kind of tissue, a process to which special attention, in its practical aspects, has recently been directed by Joseph Lister.

Consult, as to structure of blood corpuscles, ROLLET'S Article in STRICKER'S Handbook; KLEIN, in Handbook for Physiological Laboratory; and FREY'S Histology.

3. CHEMICAL CHARACTERS OF BLOOD.

We shall consider (1) the chemical composition of the corpuscles; (2) the composition of the plasma, or fluid; and (3) the gases of the blood.

a. *Chemical Composition of the Corpuscles.*

The colourless corpuscles consist of protoplasm, the composition of which is unknown. The coloured corpuscles may be divided by chemical agents into a colourless, insoluble mass, called the *stroma*, and into a reddish fluid which contains the colouring matter of the blood, known as *hæmaglobine.* When *nuclei* exist in the corpuscles, they are found in the stroma; *mineral matters* exist both in the stroma and along with the hæmaglobine; and a certain amount of *gas* is in union with the latter substance. (1) The *stroma,* at ordinary temperatures, is insoluble in weak saline solutions. At 60° C. it dissolves. Two substances may be separated from it, namely, fibrinoplastine, which will be afterwards described, and protagon. The first may be obtained by treating the corpuscles (deprived of serum as much as possible, and also freed from hæmaglobine by the action of water), first with oxygenated water, and afterwards with carbonic acid. By the action of ether, protagon and cholestrine may also be obtained. The nuclei found in some corpuscles consist of an albuminoid matter which presents a few of the characters of fibrin.

(2) *Hæmaglobine,* sometimes called *hæmatoglobuline,* or *Hæmatocristalline,* may be obtained from the blood of certain animals simply by a process of freezing. For the sake of brevity, it may be represented by the following symbol:—Hæmoglobine = $\underline{\underline{H}}$. As obtained from human blood, it appears as red lozenge-shaped and four-sided prismatic crystals. It does not crystallize with the same readiness in different species of animals. Thus crystallization is very difficult with the blood of the calf, pig, pigeon, and frog; difficult with that of man, ape, rabbit and sheep; easy with that of the cat, dog, mouse, and horse; and very easy with that of the rat and guinea-pig. $\underline{\underline{H}}$ is decomposed by all agents which modify albuminous matters, and the products of decomposition are hæmatine, a coagulable albuminoid matter called globuline, and various fatty acids, such as formic, butyric, &c. Preyer has given the following formula for $\underline{\underline{H}}$:—$C_{600}H_{960}N_{154}FeS_4O_{179}$. It is important to note that it contains 42 per cent. of iron. $\underline{\underline{H}}$ forms with oxygen

a compound called oxyhæmaglobine = $\underline{\underline{H}}O$; one gramme of dry $\underline{\underline{H}}$ absorbing about one cubic centimetre of oxygen. This oxygen may be expelled by heat, and various reducing agents. $\underline{\underline{H}}O$ is more readily crystallizable than $\underline{\underline{H}}$. Carbonic oxide also forms a combination with $\underline{\underline{H}}$, called carbonic-oxide hæmoglobine = $\underline{\underline{H}}CO$, which prevents $\underline{\underline{H}}$ from uniting with oxygen.

Some of the conditions of $\underline{\underline{H}}$ may be readily recognized by means of its spectrum, for which we are principally indebted to Stokes and Hoppe-Seyler. Thus $\underline{\underline{H}}O$ gives two absorption bands between D and E.

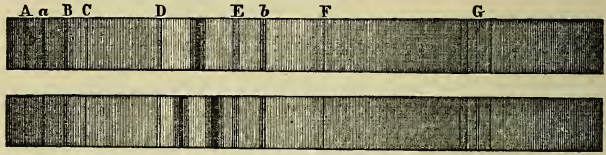


Fig. 58.—Spectra of $\underline{\underline{H}}$ and $\underline{\underline{H}}O$. The upper is $\underline{\underline{H}}$; the lower, $\underline{\underline{H}}O$.

That nearest to D is narrower than that near E. Under the influence of reducing agents, such as sulphide of ammonium, these two bands disappear, and are replaced by a single band, large, not so well defined, and which occupies the space between the two preceding. $\underline{\underline{H}}CO$ also has two absorption bands similar to those of $\underline{\underline{H}}O$, but these do not disappear under reducing agents.

(3) *Hæmatine,* having the formula $C_{34}H_{34}N_4FeO_5$, is one of the derivatives of $\underline{\underline{H}}$. It is a reddish-brown amorphous powder, insoluble in water, alcohol, and chloroform, but soluble in acidulated alcohol and the alkalies. It forms with hydrochloric acid a compound called the hæmine of Teichmann, which has been employed as a test for blood stains. In a weak alkaline solution, hæmatine has a large absorption band between C and E; treated by reducing

agents, such as sulphide of ammonium, it gives a band between D and E, and a paler one between E and *b*.

(4) *Mineral Matters.* These are the same as have been found in the plasma of blood. The corpuscles contain a considerable quantity of phosphates and of potassium salts.

b. *Chemical Composition of the Plasma.*

The plasma may be obtained in a tolerably pure state from the blood of the horse by collecting it in a vessel surrounded by a thick layer of ice. The cold prevents coagulation, or the formation of fibrin, and the corpuscles sink to the bottom of the vessel, leaving an amber-coloured fluid above, the specific gravity of which is 1027. If some of this fluid be now removed by a pipette, it coagulates into a transparent jelly The coagulum contracts so as to be surrounded by a transparent fluid, called the *serum*, whilst the coagulum is known as *fibrin.* The nature of fibrin will be described in connection with the coagulation of the blood. The *serum* is a transparent, alkaline fluid having a specific gravity of 1026 to 1029. It contains 90 per cent. of water, 8 per cent. of albuminoids, and 1 per cent. of salts. The *albuminous* matter consists chiefly of serum-albumen, a small quantity of albuminate of soda, and a trace of a substance called para-globuline. Fats exist in small amount, and consist of stearine, palmatine, and oleine. The nitrogenous substances include creatine, creatinine, urea, uric acid, and traces of xanthine, lecithine, &c. *Sugar*, as glucose, has been found in small amount. Various *fatty acids* have also been isolated. The *salts* consist of soda, potash, lime, and magnesia, as bases, combined with acids to form chlorides, sulphates, phosphates, and carbonates. The alkaline reaction of blood is due to the presence of bicarbonate of soda and the tribasic phosphate of soda. It is important to observe that salts of soda exist in excess in the plasma, whilst salts of potash chiefly abound in the corpuscles.

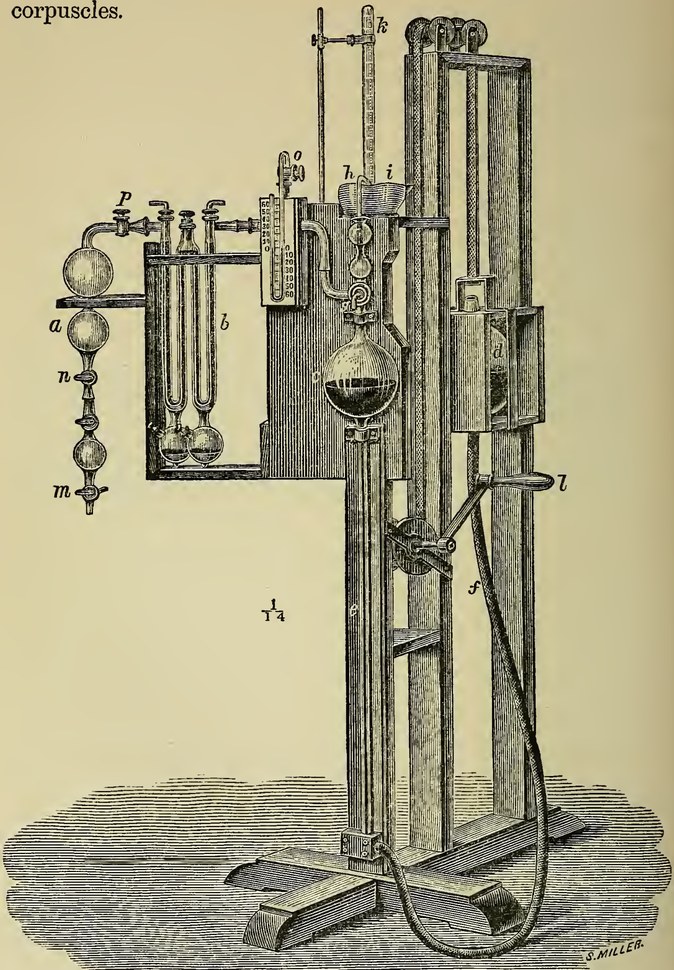


FIG. 59.—Pflüger's modification of Alvergniat's Pump for extracting the gases of the blood. This figure is copied from Gscheidlen's Physiologischen Methodik. The apparatus used in the Physiological

c. *The Gases of the Blood.*

These are removed from the blood, with the aid of heat, by means of a peculiar form of air-pump which quickly exhausts a receiver so as to allow the gases to escape in vacuo. The best form of such an apparatus is that shown in Fig. 59. It consists of a long barometrical tube, *e*, the height of which is greater than that of the ordinary barometrical column of mercury. The upper part of the tube opens into a large globe, *c*, with which two tubes, *g* and *h*, are connected; one vertical, *h*, communicating with the external air, and the other horizontal, *g*, opening into a glass vessel or receiver, *a*, into which the blood is introduced. Stopcocks are placed at the openings into the globe of these two tubes. From the lower extremity of the barometric tube, *e*, a strong india-rubber tube, *f*, passes to another globe, *d*, which may be regarded as a reservoir of mercury of greater capacity than the first globe, *c*. This reservoir may be elevated or lowered by turning a strong band, passing over a pulley, round an axle, *l*. The object of this arrangement is to extract the air from the receiver, *a*, with great rapidity. This is accomplished as follows:—Open the stopcock *g*, and shut the stopcock communicating with the receiver *a*; elevate the reservoir of mercury, *d*, above the level of the globe *c*; the air in the globe is expelled through the vertical tube *g h*; turn the stopcock of this tube at *g*, then lower the reservoir

---

Laboratory of the University of Glasgow, made by Geissler of Bonn, is slightly different, especially as regards the form of the receiver *a*. *a*, receiver for blood; *b*, U-tubes, containing asbestos and H_2SO_4 for absorption of aqueous vapour; *c*, glass globe, containing mercury, communicating with *d*, a similar globe, by glass tube *e* and india-rubber tube *f*; *h i*, mercury trough for collecting the gases in the tube *k*; *l*, handle of crank for elevating globe *d*; *m n*, stopcocks for regulating entrance into blood-receiver, *a*; *o*, pressure gauge of mercury, for ascertaining diminution of pressure in *a* and *b*; *p*, stopcock commanding the communication between blood-receiver *a* and gas-drying apparatus *b*.

as far as it will go; the mercury falls as it would do in a long barometrical tube so as to leave the globe *c* a vacuum, with the exception of some vapour of mercury; the stopcock commanding the horizontal tube of the receiver *a* is then opened and immediately the air passes from thence into the globe *c;* the stopcock at the opening of the horizontal tube is shut and that of the vertical tube opened, and, finally, by again elevating the reservoir, the gas obtained by the preceding experiment is expelled. The operation above described is repeated several times until the air in the receiver has been removed as far as possible. The next step is to introduce the blood into the receiver without allowing either to be influenced by the air, which is most readily accomplished by having an air-tight tube, communicating between the vessel of the animal and the receiver, carefully adjusted previous to the operation of exhausting the latter. When the latter has been exhausted as far as possible, a stopcock commanding this tube is turned so as to allow a fixed quantity of the blood to flow into the receiver. This having been done, communication between the vessels of the animal and the receiver is shut off, and that of the receiver with the glass globe opened, so as to allow the gases of the blood, now under a minimum of pressure, to escape. The gases pass into the globe, from which they may be expelled through the vertical tube by elevating the cistern *d*, in the manner before indicated, and they are collected in graduated tubes over mercury. By graduation, the amount of gas per volume of blood is readily ascertained. To assist in the liberation and escape of gas from the blood, the receiver is usually immersed in a water bath of about 40° C., and the liberation of carbonic acid may be further accelerated by the addition of a small amount of a hot solution of tartaric acid. The total amount of gas having been ascertained, the percentage amount of each gas in the mixture is estimated by the ordinary methods of the volumetric analysis of gases—the oxygen being absorbed by pyrogallic acid, the carbonic acid by potash, whilst the amount of nitrogen is represented by what remains.

By this method, it has been ascertained that the blood contains (at 0° C. and 1000 millimetres pressure) about 45 volumes of gas in 100 volumes; of which, in arterial blood, 14 volumes consist of oxygen, 30 of carbonic acid, and 1 of nitrogen. The nitrogen is simply dissolved in the blood, but the other two gases are partly dissolved and partly in a state of loose chemical combination with certain of the constituents of the blood. Thus, the greater part of the carbonic acid present is united with the phosphate of soda, and possibly also with the carbonate of soda, of the blood. It would also appear, as an inference from experimental data, that a small portion of the CO_2, thus in a state of combination, may be united with the coloured corpuscles, whilst the remainder exists along with salts in the serum. In like manner, part of the oxygen is simply dissolved, and the other part is in combination with the $\underline{\underline{\text{H}}}$ of the coloured blood corpuscles. As already stated, $\underline{\underline{\text{H}}}$ has a strong affinity for O, becoming oxyhæmaglobin, and this O may be set free by various reducing agents. It has been supposed that reducing agents may exist in the blood, in certain conditions, which, by their action, will convert it into venous blood. It is more probable that all active tissues act as reducing agents, so that arterial blood passing through them gives up its oxygen, and becomes venous.

When blood is exposed to carbonic acid and oxygen, these gases are not absorbed according to the law, first stated by Dalton, which regulates the absorption of a mixture of gases by a simple liquid. With such a liquid as water, the amount of gas absorbed is dependent on the specific nature of the gas, on the temperature at which absorption takes place, and on the pressure to which the gases are subjected. Where a mixture of two or more gases are exposed to such a liquid, the quantity of each gas absorbed is also dependent on the pressure which each gas exerts on the liquid. It was first pointed out by Magnus that CO_2 and O do not behave, with regard to blood, according to the law of Dalton above stated, and consequently he concluded that a portion of each gas is not simply dissolved in the fluid, but combines chemically with some constituent or constituents of the blood. Numerous researches have confirmed this opinion, and the fact may be readily demonstrated by means of the apparatus seen in Fig. 57. Thus, a certain amount of CO_2 may be obtained from blood by simply exposing it to a vacuum, whilst the remainder is liberated only after the addition of tartaric acid. The exact nature, however, of this state of loose combination is unknown. The capacity of absorption of both CO_2 and O by *serum* is nearly the same as that of distilled water.

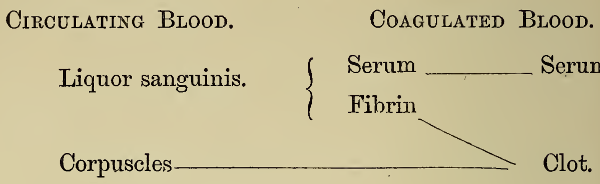
C.—THE CHANGES WHICH THE BLOOD UNDERGOES WHEN REMOVED FROM THE BODY.

When blood is removed from the body and exposed to the air and to contact with foreign bodies, it quickly separates into a solid and a fluid portion, a change known as the *coagulation of the blood.*

1. General Phenomena of Coagulation.

From two to five minutes after removal from the blood-vessel, the blood separates into a solid part termed the *clot,* and a fluid portion known as the *serum*. The form of the clot is always that of the vessel into which the blood is received, and at first it apparently completely occupies the volume of the previously fluid blood. In the course of a few minutes, however, the clot begins to shrink, and it soon separates itself from the sides and bottom of the vessel, and floats in a fluid of a straw yellow colour. The contraction of the clot usually terminates in from 12 to 20 hours. As the resistance to contraction of the clot is greatest where it touches the sides of the vessel, and least in the centre, the upper surface usually becomes concave, or, in the language of the old pathologists, *cupped*. When a clot formed in a tall cylindrical glass vessel, of narrow diameter, is examined, it will be seen that its colour increases in intensity from above downwards. Thus the surface may be nearly white, with a shade of pink, and the colour may become, by insensible graduations, deeper and deeper until the base of the clot is seen to be blood-red. The white layer thus formed is known as the *buffy coat*, and is due to the presence in that region of a preponderance of colourless corpuscles. It is best seen in blood which coagulates slowly; as, when this occurs, the coloured corpuscles, from their greater specific gravity, sink towards the bottom, leaving the lighter colourless corpuscles nearer the top.

Whilst the blood was in the body it consisted of a fluid, the *liquor sanguinis*, in which floated the two kinds of corpuscles. When coagulation takes place, a new solid substance is formed called *fibrin*, constituting the fibrous matrix of the clot, in which the greater number of the corpuscles become entangled. Clot, therefore, consists of fibrin and corpuscles, and the serum consists of fluid, holding, in suspension, only a few corpuscles, and, in solution, salts, soluble organic substances, and gases. The process may be conveniently impressed on the memory by the following diagram:—



2. PHYSICAL CONDITIONS INFLUENCING COAGULATION.

It is accelerated by the following causes: (1) the presence of oxygen; and (2) a mean temperature. The free access of air undoubtedly favours the change. This may be readily observed by contrasting the time required when the blood is collected in a large or flat vessel with that necessary in tubes or deep cylindrical vessels with narrow mouths. Blood will coagulate *in vacuo*, but the change is much delayed if precautions be taken to avoid agitation and to have the temperature of the vessel nearly that of the blood in the vessels. On the other hand, the process is retarded: (1) by the absence of oxygen; (2) by a temperature below zero or above 60° C.; (3) by saturation of the blood with CO_2; and (4) by the addition of neutral salts, such as sulphate of soda, carbonates of soda or of potash, nitrate of potash, and the alkaline chlorides. Coagulation may be prevented for a considerable time, so as to secure separation of the coloured corpuscles from the liquor sanguinis, by collecting blood, say from a horse, in a tall vessel, surrounded by ice. The liquor sanguinis, thus obtained tolerably pure, on being removed from the vessel by a pipette, and submitted to ordinary temperatures, speedily coagulates into a translucent yellowish jelly.

3. Vital Conditions influencing Coagulation.

In normal circumstances, whilst the blood is circulating through the vessels, coagulation does not take place. It would thus appear that the walls of the vessels, whilst alive, may prevent the change. As Brücke has pointed out, whilst the blood is in the vessels, many of the conditions, such as movement, friction and temperature, are the same as those which favour coagulation when the blood is removed from the body; but in normal circumstances, in addition to these conditions, the blood is in contact with *living tissue.* When the tissue dies, the blood coagulates, as may be seen in the bloodvessels of a dead animal. Occasionally, however, blood may remain fluid for a lengthened period, even in dead vessels. Nor does the blood coagulate in the smaller vessels immediately after death. It may remain fluid for hours. Coagulation first commences in the heart and larger vessels, then in those of intermediate size; whilst in the smallest, decomposition may set in without any previous stage of coagulation. Foreign bodies introduced into the current of the circulation may become covered with a layer of fibrin, and it is well known that this may also occur on any surface roughened by inflammatory deposit either on the valves of the heart or in the interior of vessels. In some pathological states, also, there is a tendency to coagulation in the cavities of the heart, or in the vessels, leading to the formation of what is called a *thrombus,* and a portion of this, detached and whirled off by the stream of blood, is known as an *embolus.*

4. Nature of Coagulation.

The old view held with regard to coagulation was that a substance called fibrin was dissolved in the blood, and in some transudations from the blood, and that in certain conditions it coagulated so as to form a clot. In 1845, Professor Andrew Buchanan, of the University of Glasgow, first clearly indicated that at least two substances were necessary for the production of fibrin, by demonstrating that certain fluids (such as that from a hydrocele), which do not coagulate spontaneously, undergo this change when a morsel of clot, or fluid expressed from the clot (serum), or a bit of muscle or of membrane, are added to it. Dr. Buchanan also recognized that two fluids, serum and hydrocele fluid, neither of which coagulate spontaneously, will form a coagulum when mixed together. Since that date, numerous researches by Schmidt of Dorpat, by Allchin, and others, have conclusively proved the truth of Dr. Buchanan's theory: the elements of fibrin have been obtained analytically, and they have been synthetically combined to form fibrin. The nature and conditions of the change will be best understood by describing briefly the characters of the substances involved.

1. *Fibrin.* This substance may be readily obtained by washing a blood clot, or by switching some blood with a bunch of twigs. It consists of white, structureless filaments, insoluble in water, alcohol, or mineral acids; soluble in lactic, phosphoric, and acetic acids; also soluble in potash, solutions of alkaline salts, and in a $\frac{1}{10}$th per cent. solution of common salt. It is decomposed by oxygenated water, splitting up into various substances.

2. *The Plasmine of Denis.* If common salt, to the point of saturation, be added to liquor sanguinis, obtained free from corpuscles, from the blood of the horse, by the application of cold, a whitish, cloudy precipitate falls. This precipitate, re-dissolved in water, soon forms a coagulum; and, according to Denis, it divides into two parts, one forming a clot, which is true fibrine, and the other, remaining in the

liquor sanguinis, which he terms soluble fibrine. On the removal of the plasma of Denis from the liquor sanguinis, the latter loses the tendency to coagulation. It would therefore appear that the formation of fibrin depends on some change occurring in this substance. The question arises as to whether or not the plasma of Denis be itself a simple substance.

3. *Fibrinogen.* If some hydrocele fluid, which coagulates on the addition of a little serum, be treated with common salt or with a stream of carbonic acid, a precipitate is obtained, on the removal of which the fluid will not coagulate on the addition of serum; but if the precipitate be added to serum, a coagulum is formed. This substance is termed fibrinogen.

4. *Fibrinoplastin.* On the other hand, the addition to saturation of common salt to serum, or the passage for a time of a stream of carbonic acid through serum diluted with twenty times its bulk of water, throws down an amorphous precipitate, which when re-dissolved, and added to hydrocele fluid, will form a clot, whilst the serum, after removal of this substance, has no such effect. This substance is termed fibrinoplastin.

Thus it may be demonstrated: (1) that a fluid containing fibrinogen alone—hydrocele fluid—will not coagulate spontaneously; (2) that a fluid containing fibrinoplastin alone—serum—will not coagulate spontaneously; (3) that fluids from which either of the substances have been removed will not coagulate on the addition of the other substance, or of the fluid which contains it; and (4) that when two fluids, the first containing the one substance, and the second the other, are mixed, fibrin is formed. Finally, as was shown by Allchin, fibrinogen and fibrinoplastin may be separately obtained by the chloride of sodium process, re-dissolved, and when the solutions are mixed, a coagulum, fibrin, is the result. In all probability, therefore, the plasma of Denis consists of these two substances. It exists, as has been pointed out, in the blood, and, in addition, both fibrinoplastin and fibrinogen, may be isolated from that fluid. The difficulty is to explain why it is that these two substances do not readily combine even in the circulating blood. Here knowledge is obscure and we pass into the region of hypothesis. It has been supposed that a third substance is necessary, in living conditions, for the fusion of the two elements of fibrin—a substance of the nature of a ferment; and it has been further supposed that during life this ferment is changed as rapidly as it is formed, so that coagulation does not take place. If, however, the ferment be not destroyed, as on death of tissue, or on the removal of the influence of tissue, it will combine fibrinogen and fibrinoplastin so as to form fibrin. The ferment has not been isolated, and the only definite fact suggesting the probability of its existence is, that colourless blood corpuscles appear to be essential to the formation of fibrin, of the appearance and of the consistence it presents in ordinary blood clot. This may appear inconsistent with the statement above made, that when fibrinogen and fibrinoplastin are separated by the chloride of sodium or carbonic acid processes, fibrin is produced; but it must be remembered that these processes may separate the ferment as well as the two other factors.

Consult ANDREW BUCHANAN's original papers in London Medical Gazette, April, 1836; and proceedings of Glasgow Philosophical Society, March, 1844 and 1845; LISTER, Proceedings of the Royal Society, 1863; A. SCHMIDT, in REICHERT and DU BOIS-REYMOND's Archiv, 1861, and in PFLÜGER's Archiv, 1872–1876; also Hämatologische Studien, Dorpat, 1865. See also FOSTER's Physiology, p. 14; BURDON-SANDERSON, in Handbook for Physiological Laboratory; and WUNDT's Physiologie, p. 229. JOHN HUNTER's Article on Inflammation should also be referred to. See his works, edited by PALMER, vol. I.

D.—THE CIRCULATION OF THE BLOOD.

The blood, which in an adult probably amounts to about $\frac{1}{14}$th part of the weight of the body, is contained during life in a continuous system of more or less elastic vessels. Anatomically, these consist of (1) the arteries, terminating in (2) the capillaries, from which originate (3) the veins; whilst a special contractile organ (4) the heart, is placed at the commencement of the arteries and the termination of the veins. The general arrangement is seen in Fig. 60.

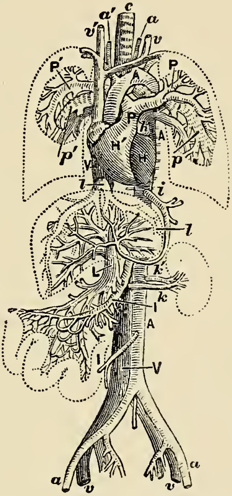


Fig. 60.—Diagram showing generally the course of the Circulation and some of the principal vessels: H', right ventricle; H, left ventricle; A, A, A, aorta; *k* part of left auricle; P, pulmonary artery going to lungs; *v*, ascending or lower vena cava; *e*, trachea or windpipe; *a'*, *a*, right and left carotid arteries; *v'*, *v*, veins from root of neck (internal jugular and subclavian) joining to form descending or upper vena cava; *i*, hepatic artery; *l*, hepatic vein; I, superior mesenteric artery going to mesentery and bowels; L, portal vein going to liver; *k'*, renal artery; *k*, renal vein; V, inferior vena cava splitting into the two iliac veins.—Allen Thomson.

The heart may be regarded as a double organ, each half consisting of an auricle and a ventricle, the right half containing blood which has been returned from the body to be sent to the lungs, and the left half containing blood which has been returned from the lungs to be distributed to the body. There are thus, in a sense, two circulations; the one, *pulmonary*, from the right side of the heart, by the pulmonary artery to the lungs, through the capillaries of the lungs, and back to the left side of the heart by the pulmonary veins; and the other, *systemic*, from the left side of the heart, by the aorta, and the arteries which ramify from it, to the capillaries throughout the tissues, and from thence by the veins to the right side of the heart. Thus the *course* of the circulation may be traced from right auricle to right ventricle, through right auriculo-ventricular opening, guarded by the tri-cuspid valve; from right ventricle by pulmonary artery, through the capillaries of the lungs, to the pulmonary veins which open into the left auricle; from left auricle to left ventricle, through left auriculo-ventricular opening, guarded by the mitral valve; from the left ventricle into the greater arteries, the medium-sided arteries, and the arterioles into the capillaries of the tissues and organs, and from thence by the veins, opening into larger and larger trunks so as ultimately to constitute the superior and inferior venæ cavæ, which open into the right auricle, from which we started. Remembering that the walls of these tubes are all more or less elastic, imagine them to be filled with a considerable amount of fluid; we would then have a condition of permanent tension, which would be varied if pressure were applied to any part of the system. Such a variation of pressure would produce a movement, or, in other words, a *circulation*, and by mechanical arrangements of valves, the movement might be always in the same direction. In the living body, the contractions of the heart force blood into the arterial system so as to increase pressure in that part of the circulation; the arteries empty part of their contents into the capillaries which carry the blood to the veins, so as to tend to an equalization of pressure between the venous and arterial systems; if the pressure in both systems became equal, there would be no circulation, but as the veins pour a portion of the blood back again into the heart, this organ again contracts so as to prevent the possibility, during life, of an equalization of arterial and venous pressure. Thus movement, or circulation, goes on.

The fact that there is a complete circulation of the blood was first demonstrated by WILLIAM HARVEY in 1628.

We shall describe (1) the action of the heart; (2) the action of the vessels; and (3) the relation of the circulation to the volume of other organs.

1. THE ACTION OF THE HEART.

The heart may be regarded as a hollow muscle, of which the external surface is covered by a serous membrane, the *pericardium*, whilst the interior is lined by another serous membrane, the *endocardium*. It is situated in the left half of the chest, and it is placed obliquely in three directions—namely, from above downwards, from right to left, and with reference to its own median plane. The base corresponds to the bodies of the sixth, seventh, eighth, and ninth dorsal vertebræ, and its apex is situated behind the sixth costal cartilage on the left side. With the general form of the cavities, the arrangement of the vessels, and the muscular structure of the heart, the student is presumed to have made himself familiar in his anatomical studies.

Consult QUAIN, vol. II., p. 242. For original observations as to the size and weight of the heart, see JOHN REID'S paper in the

Edinburgh Monthly Journal of Medical Science, April, 1843; and a paper by J. B. PEACOCK, in the same Journal, in 1846.

The pericardium is adherent below to the upper surface of the diaphragm, so that the heart follows, within certain limits, the ascent and the descent of that muscle.

a. *Modes of Examining the Heart.*

When the hand is applied to the side, a little to the left of the left nipple, and in the interval between the fifth and sixth ribs, a shock or impulse is experienced. In some rare cases, where there was a congenital fissure of the sternum, the finger could be applied to various parts of the heart's surface. This mode of examination may be termed *palpation.* Again, when the ear is applied either directly, or indirectly by means of a stethoscope, over the position of the heart, sounds are heard, the duration and rhythm of which are of physiological importance. This mode is known as *auscultation.* The direct registration of the movements of the heart has been accomplished with the aid of instruments termed *cardiographs,* of which the most convenient form is that of Marey, seen in Fig. 61.

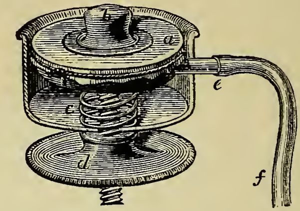


FIG. 61.—Section of the Cardiograph of Marey for recording the movements of the heart of man or of animals. *a*, india-rubber membrane; *b*, vulcanite or ivory knob applied over the apex of the heart, resting on a thin aluminium plate; *c*, spiral, which may be tightened or relaxed by turning the milled head *d*, thus increasing or diminishing the sensibility of the instrument; *e*, *f*, tube leading to the registering tambour.

The adjustment of the apparatus with a registering tambour is seen in Fig. 62.

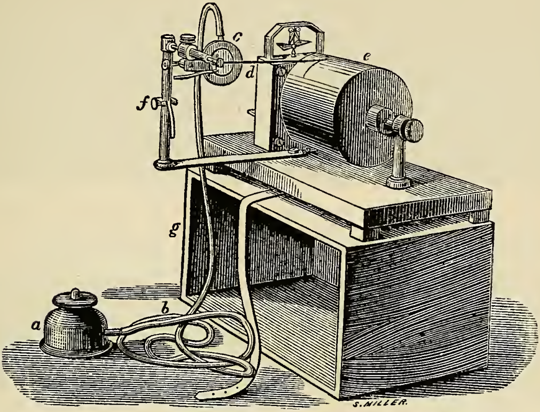


Fig. 62.—Arrangement of apparatus for recording movements of the heart by the cardiograph of Marey. *a*, cardiograph; *b*, tube, communicating with *c*, recording tambour; *d*, clockwork, moving cylinder *e*; *f*, fine adjustment screw for bringing lever of registering tambour on surface of cylinder at the proper time; *g*, box, in which the whole instrument may be packed.

The following are examples of tracings obtained by this method :—

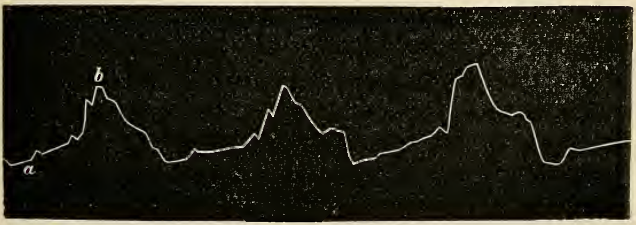


Fig. 63.—Tracings of the cardiac pulsations of a healthy man. (*Marey.*) The differences in form between the first two and the last pulsation are due to respiratory influences.

Fig. 64.—Tracings of the cardiac pulsations of a man suffering from a febrile affection. (*Marey.*) Observe the irregularities of the curve as contrasted with Fig. 63.

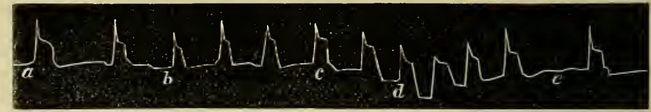


Fig. 65.—Tracings of the cardiac pulsations of a dog. (*Marey.*) Observe the general similarity in form between Fig. 65 and Fig. 63.

The movements of the heart of a cold-blooded animal, such as the frog, may also be studied after removal from the body, and tracings of even so small an organ may be obtained, by the arrangement shown in Fig. 32, p. 129.

b. *General Characters of the Movements of the Heart.*

The movements of the heart consist of a series of contractions which succeed each other with a certain rhythm. The period of contraction has received the name of the *systole,* whilst that of the relaxation is known as the *diastole.* The two auricles contract and relax synchronously, and these movements are followed by a simultaneous contraction and relaxation of the ventricles. Thus, there is a systole and a diastole of the auricles, and a systole and diastole of the ventricles. On the other hand, if we consider each half of the heart, the contractions and relaxations of the auricle, and the contractions and relaxations of the ventricle are successive. Finally, there is a very short period in which the heart is entirely in diastole. The whole series of movements, from the commencement of one auricular systole to the commencement of the one immediately following has received the name of the *cycle,* or *period of revolution* of the heart, and the sequence and duration of the various movements may be fixed on the memory with the aid of the following diagram :

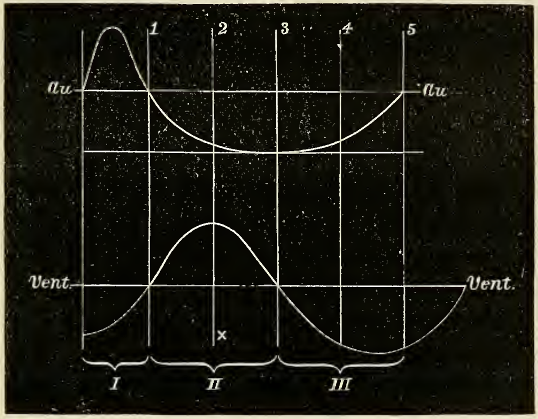


FIG. 66.—Diagram of the movements of the heart. Modified from *Beaunis, Wundt,* and *Landois.* For description see text.

In this diagram, the systole is represented by a curve above the horizontal lines and the diastole by a curve below these; the auricular changes are traced on the upper line, *au—au,* and those of the ventricle on the lower line, *vent—vent.* The length of the lines represents the total duration of a cardiac revolution. On examining this diagram, it will be seen that the auricular systole occupies $\frac{1}{5}$th part of the total time of a revolution of the heart, and the ventricular systole

$\frac{2}{5}$ths; that the auricular systole immediately precedes the ventricular systole; that the commencement of the ventricular systole coincides with the commencement of the auricular diastole, and that during $\frac{2}{5}$ths of the total period, both auricles and ventricles are in a state of diastole. There are thus three periods to be considered: (1) a period of auricular systole, $\frac{1}{5}$th; (2) a period of ventricular systole, $\frac{2}{5}$ths; and (3) a period of repose, $\frac{2}{5}$th. The impulse of the apex against the walls of the chest, the moment of which is indicated in the diagram by a ×, occurs at the middle of the time occupied by the ventricular systole.

In 1861, Chauveau and Marey succeeded in obtaining a direct record of the various movements of the heart of a horse by introducing into the right cavities, auricle and ventricle, small oval pressure-bags filled with air and which were connected with registering tambours. These, along with a third tambour connected with a cardiograph applied to the chest over the apex of the heart, were adjusted in the same plane to a blackened surface on a revolving cylinder. The tracing is seen in Fig. 67, and ought to be carefully studied, not only as giving a history of the cycle of changes occurring in the heart, but as being one of the most beautiful applications of the graphic method of registering physiological phenomena with which we are acquainted.

Observe, in the tracing, an illustration of the following points: (1) The auricular contraction is less sudden than the ventricular, as indicated by the line *a b* being more oblique than the line *c′ d′*; (2) The auricular contraction lasts only for a very short time, as shown by the curve almost immediately beginning to descend, whereas the ventricle remains contracted for a considerable time, and then slowly relaxes; (3) The time of the contraction of the auricle and of its relaxation are about equal, but the time of the relaxation of the ventricle is nearly twice as long as the time of its contraction: the movements of the auricle are thus uniform and wavelike, whilst those of the ventricle are more of a spasmodic character; (4) The auricular movement, as already stated, immediately precedes the ventricular, and the latter coincides with the impulse of the apex against the wall of the chest, as may be seen by allowing the eye to follow the second

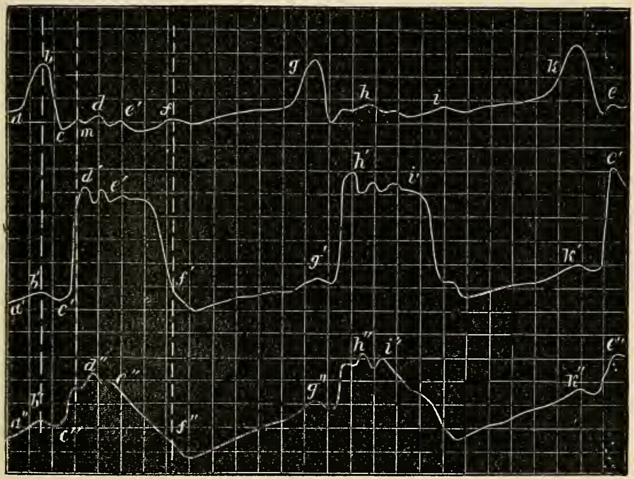


FIG. 67.—Tracings obtained from the heart of a horse by Chauveau and Marey. The upper tracing is from the right auricle, the middle from the right ventricle, and the lower from the apex of the heart. The horizontal lines represent time, whilst the vertical represent amount of pressure. The vertical dotted lines mark coincident points in the three movements. The breadth of one of the small squares = $\frac{1}{10}$th of a second. For further description see text.

vertical dotted line; (5) The contraction of the auricle, by forcing blood onwards, affects the pressure for an instant in the ventricle, as indicated by the little elevation seen immediately before the ventricular contraction; and lastly, (6) During the period of contraction of the ventricle, there are oscillations of pressure affecting both the auricle and the ventricle which are indicated by the little waves *d e*, *d' e'*,

d'' and e'' on the three lines: similar waves are seen in the other curves, at h i, h' i', and h'' i''.

We must still study a little more closely the phenomena occurring in the heart so far as the *blood* is concerned.

Suppose the blood to be pouring from the venæ cavæ and from the pulmonary veins into the two auricles. At that time, the auricles are passing into a state of complete diastole, and their cavity is increased by the funnel-shaped aperture at the auriculo-ventricular openings formed by the segments of the valves guarding these orifices. It is also to be noted that during this time both ventricles are filling with blood, the auriculo-ventricular orifices being open. When the distension of the auricles is complete, the auricular systole commences as a rhythmic contraction at the orifices of the veins, which is afterwards propagated through the whole of the auricle. The contracting wall forces the blood chiefly in the direction of least resistance, that is into the ventricle, which at that time is only partially full of blood, and is passing into a state of complete relaxation. The pressure in the veins, aided by the rhythmic contraction made by them at the commencement of the auricular systole, is quite sufficient to prevent the blood from passing backwards, except to a very slight extent. It is thus seen that the auricles act not only as passive reservoirs for the blood in its passage from the veins to the ventricles, but as rhythmic cavities tending to keep up a mean pressure in the veins, in diminishing by their extensibility the pressure which tends to increase during the ventricular systole, and in increasing it by their contraction at a time when the venous pressure would diminish, that is, towards the close of the ventricular diastole.

The amount of blood discharged into the ventricles (already partially filled during the relaxation of the auricles) by the auricular systole is sufficient to fill their cavities, and consequently, the ventricular systole immediately follows the contraction of the auricles. When the ventricles contract, the musculi-papillares act at the same time, so as to bring the edges of the auriculo-ventricular and mitral valves into close contact, an arrangement which prevents the passage of blood backwards into the auricles. The blood thus compressed can only pass into the pulmonary artery from the right, and into the aorta from the left, ventricles. As it passes, the segments of the sigmoid valves are pressed against the walls of the vessels, and as both the pulmonary artery and aorta contained a certain amount of blood before, the pressure in these vessels is increased, and the walls of both yield to a considerable extent. As already stated, the ventricle continues in the contracted state for a brief space of time, and then it relaxes. Simultaneously with the commencement of relaxation, the auriculo-ventricular orifices open, thus permitting the passage of blood from the auricles; and at the same time, the elastic walls of the aorta and pulmonary arteries recoil so as to force a portion of the blood backwards toward the cavities of the ventricles, in which, as they are passing into diastole, the pressure is much less than in the vessels. This blood, however, by filling the sinuses of Valsalva and the crescentic pouches of the sigmoid valves, closes these valves so as to prevent any blood from passing into the ventricles. It is probable that the elasticity, both of the auricular and of the ventricular walls, must exert a kind of aspiration or sucking action which will expedite the filling of these cavities. The influence of the movements of the chest will be discussed in treating of the mechanism of respiration.

c. *Shock of the Heart.*

At the time of ventricular systole, the form of the heart changes: in place of being an oblique cone, having an elliptical base, as in rest, it becomes a right cone, having a circular base; and the longitudinal and transverse diameters of the ventricular portion diminish, whilst the antero-posterior increases. The heart also rotates on its long axis from left to right, so as to expose partially the left ventricle. At the same time, the apex performs a gliding movement against the thoracic walls. This gliding movement, called the *shock* or *impulse*, is synchronous with the ventricular systole, as may be seen in Marey's tracings. It has been supposed by some, such as Ludwig, that these movements of the heart, as a whole, may be due to a twisting movement of the aorta in the longitudinal direction when the ventricle throws a quantity of blood into it.

d. *The Heart considered as a Muscle.*

Marey has shown, by a series of beautiful researches, that the form of the curve obtained by a systole is that of a muscular contraction; that fatigue diminishes the amplitude and increases the duration of the contraction, just as happens with a muscle, and that the effects of heat and cold are also similar. He has also ascertained the period of latent stimulation of the heart of the frog to be about the $\frac{1}{5}$ of a second, a much longer time than the $\frac{1}{100}$th of a second, the period of latent stimulation obtained on exciting the muscles of the leg.

e. *Decomposition of a Cardiographic Tracing into its Several Elements.*

By placing the heart of a tortoise under the lever of an apparatus similar to what is shown in Fig. 32, p. 129, Marey obtained the following tracing:—

FIG. 68.—Tracing of the pulsation of the heart of a tortoise. *a*, *b*, duration of the first ventricular systole ; *b*, *a′*, the diastole ; *a′*, *b′*, the second ventricular systole. (*Marey.*)

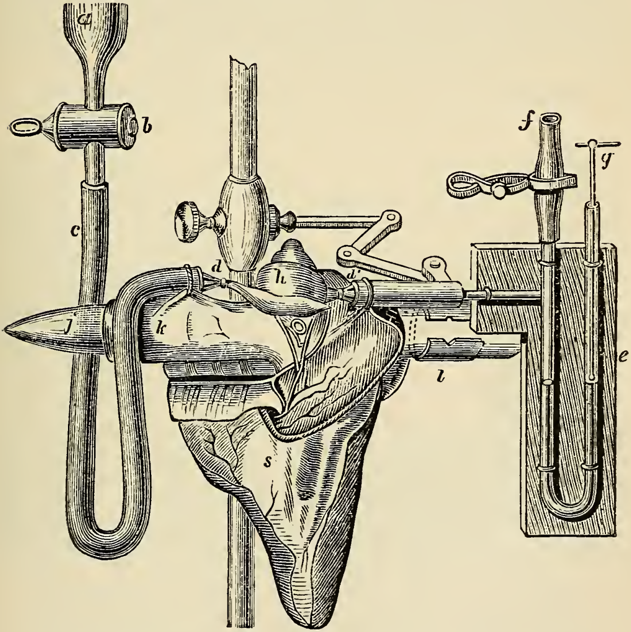


FIG. 69.—Coats' apparatus for studying the movements and pressure of the heart. *a*, *c*, tube conveying serum to the heart ; the serum passing into inferior vena cava at *d* ; *b*, stopcock. Connected with the aorta *d′* there is a small mercurial manometer *e*, which writes the movements and the pressure by the marker *f*, *g*. In this apparatus, the heart forces the blood back again into the tube *a*, and thus there is no true circulation.

It is not only interesting and instructive to analyse the elements of this curve, but the study of Marey's mode of doing so, is an excellent example of the application of scientific methods to physiological research. Ludwig and Coats were the first to introduce the method of studying and recording the movements of the isolated heart by establishing in connection with it an artificial circulation of serum. The apparatus used by Coats is seen in Fig. 69.

Marey modified the method, so as to obtain the following indications: (1) the changes of volume of the heart with each of its systoles; (2) the changes of pressure of the blood in the vessels; and (3) the quantity of blood passing in a given time. Fig. 70 shows the apparatus he employed.

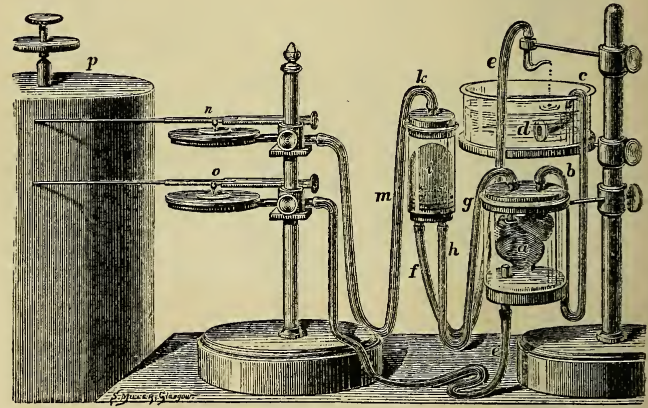


FIG. 70.—Apparatus for measuring the changes in volume of the heart during the phases of systole and diastole, with the changes of pressure which the systolic effort produces. (*Marey.*) *a*, Heart of tortoise in air-tight glass vessel, supplied with defibrinated blood from cistern *c*, by the tube *d b*, and sending blood, when it contracts, by the tube *g h*, into a small and very thin india-rubber bag *i*, in the air-tight vessel *k*; the blood passes from this bag *i* to the cistern *c*, by the tube *f e*—the heart, by its rhythmic contractions, keeping up a circulation. The tube *e*, communicating with the air-tight glass vessel, registers on the cylinder *p*, by the tambour *o*, the *changes of volume* of the heart *a*, whilst the tube *k m*, communicating with the tambour *n*, registers the *changes of pressure* in the thin india-rubber bag *i*. By graduating the

cistern *c*, the *amount* of blood passing in a given time could also be measured. It is quite evident that the deficiency, both in Coats' and Marey's arrangement, is that *the wall of the heart itself* is not supplied with blood. If this could be arranged, the action might go on for a very lengthened period.

By this apparatus, Marey obtained first the changes of volume of the heart, as seen in the following curve:—

FIG. 71.—Curve of the changes of volume of the heart of a tortoise placed in the apparatus, Fig. 70. (*Marey.*) *a b*, period of ventricular systole = diminution in the volume of the heart. *b a'*, period of diastole = increase of volume.

To measure the pressure exerted on the blood by the contracting ventricular wall with great accuracy would have necessitated the introduction of a manometer into the small cavity, a very difficult proceeding, Accordingly, he measured it approximately, by estimating the change of consistence of the ventricular wall, by pressing against it a narrow blunt body which recorded its movements by a tambour. Thus he obtained the following curve:—

FIG. 72.—Curve of changes of pressure of the ventricles measured by the resistance which the organ opposed to compression from an external cause. *a b*, hardening during systole, which increases towards the end of systole; *b a'*, state of softness during diastole.

Having thus obtained the two elements, change of volume of the ventricles and changes of pressure of the blood in its cavities, in two distinct curves, he combined them so as to reproduce the original tracing seen in Fig. 68. He superimposed the curve of change of pressure on the curve of change of volume, so that the change of pressure coincided with the systolic period, as it manifestly must do, and the result was as follows:—

Fig. 73.—Reproduction of the pulsation of the heart of a tortoise by the addition of the curve of change of volume to that of change of pressure. The dotted line is obtained by adding to the part *a b* of Fig. 71 the portion *a b* of Fig. 72. (*Marey.*)

From these data, and many others of a similar kind, Marey has succeeded in constructing an apparatus which not only artificially produces the form of curve characteristic of cardiac contractions, but imitates, with great exactitude, other cardiac phenomena.

f. *Frequency of the Cardiac Pulsations.*

These, in the adult, number from 65 to 75 per minute. Each pulsation lasts about 35 seconds, as may be seen by

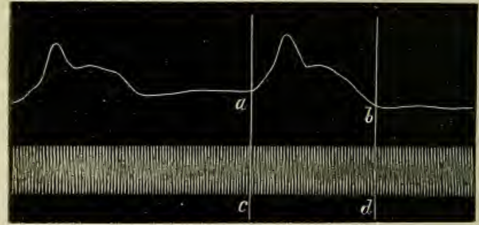


Fig. 74.—Time of individual cardiac pulsations. Chronograph = 100 vibrations per second.

referring to Fig. 74, which is an exact copy of tracings obtained by a cardiograph and a chronograph.

The number of pulsations diminishes from morning to mid-day, after which it again rises; it is increased by food, by muscular exercise, by rising from the horizontal to the vertical position, by heat, &c. There is also a distinct relation between the *quantity* of blood in circulation and the frequency of the beats of the heart. Thus, according to Vierordt:—

	Quantity of Blood per Kilog. and per Minute.	Number of Pulsations per Minute.
Horse,	152	55
Man,	207	72
Dog,	272	96
Rabbit,	620	220
Guinea-pig,	892	320

g. *Quantity of Blood in the Heart.*

From a heart of average size, each ventricular systole ejects about 180 grammes. This is the figure usually given, but it must be regarded merely as approximative. The amount may even vary in the same individual according to the state of vigour of the muscular walls of the organ.

h. *Mechanical Work of the Heart.*

This may be ascertained by the following calculation: Each systole of the left ventricle forces into the aorta 180 grammes of blood; the pressure in the human aorta has been estimated at 20 centimetres of mercury—that is, it would support a column of mercury of that height; 20 centimetres of mercury = $2\frac{1}{2}$ metres of blood; as the heart must overcome this pressure, the work done by each systole is as if it raised

180 grammes of blood $2\frac{1}{2}$ metres high—that is, $180 \times 2\frac{1}{2} = 0{\cdot}45$ kilogrammetres; say 70 systoles per minute $= 0{\cdot}45 \times 70 = 31{\cdot}50$ kilogrammetres per minute $= 31{\cdot}50 \times 60 = 1890$ per hour $= 1890 \times 24 = 45360$ kilogrammetres per day. As the pressure in the pulmonary artery is much more feeble than in the aorta, the work done by the right ventricle may be set down as $\frac{1}{3}$ of that of the left—thus

Work done by left ventricle = 45,360 kilogrammetres.
Work done by right ventricle = 15,120 ,,
Total cardiac work 60,480 ,,

In other words, the work done by the heart, in 24 hours, is equal to that done in raising 60,480 kilogrammes 1 metre high, or 1 kilogramme, 60,480 metres high. The work done is thus enormous, amounting, as will be seen in discussing nutrition and animal heat, to about $\frac{1}{5}$th of the total work accomplished by the body.

i. *Sounds of the Heart.*

When the ear is applied over the cardiac region of the chest of a healthy man, two sounds are heard, the one with greatest intensity over the apex, and the other over the base, of the heart. The sound heard with greatest intensity over the apex has received various names, such as the first, the long, the inferior, and the systolic sound, whilst that over the base has been called the second, the short, the superior, and the diastolic sound. It is impossible to describe these sounds accurately for any practical purpose; the student must hear them for himself by listening to a healthy heart. He should do this with the aid of a stethoscope and with stillness and freedom from distraction. Suppose the sounds expressed by the syllables *lupp*, *dupp*, he will notice that the accent is on *lupp* (the first sound) when the stethoscope is over the apex: thus *lúpp, dupp, lúpp, dupp;* and over *dupp* (the second sound) when over the base—thus: *lupp, dúpp, lupp, dúpp.* He will also observe a pause between the second sound and the next succeeding first sound—thus:

> At apex—lúpp dupp (pause) lúpp dupp (pause) lúpp dupp.
> At base—lupp dúpp (pause) lupp dúpp (pause) lupp dúpp.

There is no appreciable pause between the first and second sounds. It is difficult to state the *causes* of these sounds. Some have supposed that the first is due to vibrations of the auriculo-ventricular valves; others that it is muscular, owing to contraction of the ventricles; not a few have attributed it to movements of the blood through the aortic and pulmonary orifices; whilst the remainder have imagined that the sound might be the result of a fusion of these effects. It is certainly not due to the shock of the heart against the chest, as it may be heard in the heart of the dog after removal from the chest. The sound has not the quality likely to proceed from vibrating membranes or from the rush of fluid through an orifice, and it is difficult, on acoustical principles, to conceive a fusion of the supposed causes. It is not likely that the vibrations caused by movements of the valves, by muscular contractions, and by the rush of blood into the aortic and pulmonary orifices are precisely similar in number, or that the sounds produced by these causes are members of a harmonic series, by the combination of which a tone of the pitch and quality of the first sound is produced. The most likely hypothesis is that it is a muscular sound, varying in quality from the ordinary muscular sound from the peculiar arrangement of the cardiac fibres, acting on an incompressible fluid in a confined space and which can escape by only one aperture; and this view is supported by the fact that any pathological state which affects the cardiac wall, such as occurs in typhoid fever, weakens and may even remove the first sound.

It may be objected to this view that derangements of the valves affect the first sound, and that therefore it cannot possibly be due to muscular action alone. But the passage of fluid through an orifice such as is formed by diseased mitral valves is quite sufficient to produce a sound which will entirely mask the normal sound; and it has always appeared to the author that the blowing sound heard with disease of the valves is an abnormal sound entirely different from the normal first sound, and of sufficient intensity either to mask it entirely, or to produce a sound of the intensity and quality characteristic of a blowing murmur. He is also inclined to think that the proper sound of the heart in normal circumstances is only an insignificant factor in the production of a blowing murmur.

Less doubt exists as to the cause of the second sound which appears to be associated with the closure of the sigmoid valves. If one of these valves be hooked up by a curved needle, as was done by Williams, the sound disappears, whilst it returns when the needle is withdrawn. For practical purposes, and irrespective of the *causes* of the sounds, the student should familiarize his mind with what is occurring in the heart during the time occupied by each sound. Thus, with the *first* sound, we have (1) contraction of the ventricles; (2) closure of the auriculo-ventricular valves; (3) rushing of the blood into the aorta and pulmonary artery; (4) the impulse of the apex against the chest; and (5) filling of the auricles: with the *second* sound, (1) closure of the semi-lunar valves from the elastic recoil of the aorta and pulmonary artery; (2) relaxation of the ventricular wall; and (3) opening of the auriculo-ventricular valves so as to allow the passage of blood from auricle to ventricle: with the *pause* (1) gradual re-filling of the ventricle from the auricle;

and (2) contraction of the auricle, so as to entirely fill the ventricle.

j. *Innervation of the Heart.*

1. *Intrinsic Ganglia.*—If the heart of a decapitated frog be removed from the body, it will continue to beat for some time, although it has been thus removed from the influence of the great nervous centres. Rhythmical movements, therefore, may continue for a time independently of these centres. If we then cut off the apex of the heart, it will remain motionless whilst the larger portion will still beat rhythmically. Successive slices may then be removed from the larger portion without affecting rhythmical contraction until a section is made in the auriculo-ventricular groove, when it ceases in both portions. Stannius has analysed these phenomena with great care, and has shown that in the heart of the frog, at all events, there are ganglionic centres, having independent functions, one class acting simply as *reflex* centres; a second, called *accelerating* centres, which seem to quicken the cardiac movements; whilst a third, named *inhibitory*, retard or even arrest these movements. Thus, rhythm may depend on the first alone, but the amplitude, and the time of the rhythmic contractions may be regulated by other centres.

2. *Inhibitory Influence of the Pneumogastric.*—But although the heart contains intrinsic ganglia, it is also influenced by the cerebro-spinal system, as shown by its palpitations under the influence of emotion. Anatomically, it is known to receive branches from the pneumogastric and from the sympathetic nerves. In 1845, E. Weber made the remarkable discovery that excitation of the trunk of the pneumogastric in the neck produces, if the excitation be feeble, a diminution of the number of cardiac beats, and if it be strong, arrest of the heart in diastole with repletion of all

its cavities. Section of the nerves he found to be followed by an acceleration of the pulse. The slowing and the arrest of the heart may be produced by electrical, mechanical, or chemical stimulation. In man, Czermak observed that compression of the carotid (a very dangerous experiment) at the anterior border of the sterno-mastoid was followed by slowing of the heart, an effect which he attributed to irritation of the pneumogastric. The arrest of the heart produced by electrical stimulation of the pneumogastric lasts from fifteen to thirty seconds in the dog. During arrest, the heart has not lost its excitability, and it will respond to direct stimulation. The stoppage cannot be regarded as a reflex act; it is direct, inasmuch as it will take place on stimulating the distal end of the cut nerve. Various observers have stated that very gentle stimulation is followed by quickening of the cardiac movements, and they are disposed to regard the slowing as a kind of paralytic effect; but there can be no doubt that these views arose from errors of the experimental methods they employed, as it is impossible to stimulate the pneumogastric nerve, be it ever so gently, without the result of slowing the heart's pulsations. The acceleration of the beats of the heart which follows section of the pneumogastrics may be readily observed in animals of slow pulse, such as frogs, tortoises, turtles, &c. The right vagus exerts a more powerful influence on the heart than the left.

But the pneumogastric acts not only on the frequency of the cardiac beats, but upon the amplitude of the pulsations. When stimulated, the pulsations not only become fewer, but also more feeble, so that, according to Coats, the work of the heart, in a given time, is diminished.

Section of the spinal cord, and of the two sympathetics in the neck, increase the excitability of the pneumogastric, so that an extremely feeble irritation is sufficient to arrest the heart's action. It has also been ascertained that *atropine* paralyses the cardiac action of the pneumogastric; *nicotine* has the same effect after a period of excitation: *muscarine*, on the contrary, excites the pneumogastric and stops the heart in diastole; *upas antiar* and *veratrine* have a very energetic action, a large dose causing a tetanic state of the ventricles; and *physostigmine* slows the heart's action, and arrests it in diastole. Some of these substances undoubtedly act on the intrinsic ganglia of the heart. It is probable that the vagus acts on some of the cardiac ganglia, and not on the muscular fibres directly.

Thus, certain fibres in the pneumogastric exercise an *inhibitory* or restraining influence over the cardiac pulsations, but the exact mechanism by which they do so is still unknown. The action, as recorded by a cardiograph, is shown in the following tracing by Marey.

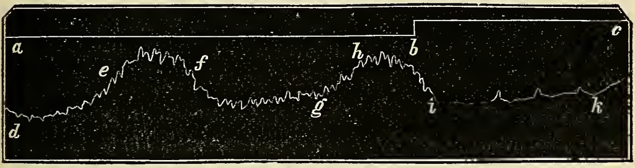


FIG. 75.—Cardiographic tracing from a rabbit. The two pneumogastrics had been cut. At the point *b*, as indicated by the inflection of the electric signal, *a*, *b*, *c*, the peripheral end of one pneumogastric was stimulated, and the effect, from *i* to *k*, is almost complete arrest of the movements of the heart. The tracing is to be read from left to right.

3. *Action of the Sympathetic.*—This nerve contains fibres which apparently act antagonistically to the inhibitory fibres of the vagus, that is, they are *accelerators*. Section of the sympathetic, even on one side, is followed by slowing of the heart's action, whereas stimulation of the peripheral end causes the beats to become faster. Stimulation also of the delicate fibres passing to the heart from the inferior cervical

ganglion causes an acceleration of the beats of the heart. These accelerating fibres originate, it is believed, in the spinal cord, as it has been found that even after dividing all nervous communications between the heart and the cerebro-spinal centres, and leaving only the accelerating fibres of the sympathetic intact, even then stimulation of the upper end of the cord will cause acceleration of cardiac beats. It has also been ascertained that stimulation of the two first dorsal ganglia of the sympathetic quickens the beats of the heart. The accelerating fibres, then, augment the number of the heart's pulsations, but they do not appear to alter the amount of work done by the heart. Consequently, in a strict sense, they cannot be regarded as the *motor* nerves of the heart. Moreover, severe excitation does not produce tetanus as it would do if they were motor nerves distributed to muscular fibres. They end, probably, in intra-cardiac ganglia, reinforcing, in some manner unknown, their automatic activity.

4. *Reflex Action of some Fibres of the Sympathetic.*—The sympathetic, in addition to accelerating fibres, contains also centripetal fibres, which excite reflex activity through the vagi. If, in a rabbit, the two sympathetic nerves be divided in the lower part of the neck, and the cephalic end be excited, there is slowing of the pulse, a result which will not take place, however, if the vagi have been previously cut. The sympathetic in the abdominal region appears also to contain fibres, the excitation of which slows the heart's beats, through the medium of the vagi. Thus, as shown by Goltz, a sudden stroke on the stomach may, in this way, stop the action of the heart, a fact which may account for sudden death from syncope after a blow on the epigastrium, or after swallowing ice-cold liquids or corrosive poisons. François-Franck has also shown, in an elaborate research on the effect on the heart of excitations of sensory nerves, that sudden and

severe stimulation of almost any nerve may produce such an effect. The following is one of his illustrations :—

FIG. 76.—Slowing of the action of the heart caused by pinching of the posterior auricular nerve at the point indicated by the vertical dotted line. Tracing to be read from left to right. At *e*, the irritation was removed.

5. *Action of the Spinal Cord on the Heart.*—As already stated, there can be no doubt the accelerating fibres originate in the upper part of the cord. The *medulla oblongata* contains the inhibitory centre for the pneumogastric, but the exact situation of the centre has not been well determined. Stimulation of the medulla is said to be followed by arrest of the cardiac beats. It would appear, therefore, that in the medulla and upper part of the cord there are two centres related to the heart—(1) an *inhibitory* centre, which gives origin to the inhibitory fibres of the pneumo-gastrics ; and (2) an *accelerating* centre, which is connected with those fibres passing through the sympathetic that quicken the heart's movements. It has also been observed that the inhibitory centre is at once excited by the presence of an undue amount of carbonic acid in the blood. For example, if the nostrils of a rabbit be compressed for a few seconds, the heart beats more slowly. Again, oxygen excites the accelerating centre. Thus the two centres may each be excited either by the state of the blood or by nervous influences. These nervous influences may be of two kinds : (1) those coming from the periphery of the body (*sensory nerves*), from the abdominal cavity (*splanchnics*), or from the heart itself by a special nerve to be presently alluded to (the *depressor*) ; and (2) those coming from the higher cerebral centres, the action of

which explains the influence of emotional states on the heart.

6. *Action of Depressor Nerve.*—The action of this nerve, sometimes called the *nerve of Ludwig and Cyon,* will be better understood after studying the circulation in the vessels and the innervation thereof.

2. The Action of the Bloodvessels.

For a description of the minute structure of bloodvessels, arteries, veins, and capillaries, see QUAIN'S Anatomy, vol. II., p. 163. A few words here are sufficient. Ultimate capillaries may be regarded as being composed of a simple tissue, consisting of flattened cells, the edges of which may be noticed after being darkened by the action of nitrate of silver. A layer of flattened cells, similar in many respects to those forming the ultimate capillaries, constitute the so-called endothelial lining of vessels, seen in Fig. 77. All the other vessels consist, as already stated, of a layer of flattened cells, around which there are layers of elastic, muscular, and connective tissues, of greater or less thickness. These adventitious coats may be divided, for convenience, into two: (1) a middle coat, consisting of involuntary muscular fibres interspersed with connective tissue (the so-called *muscular coat*); and (2) an external coat, formed of connective tissue mixed with elastic fibres (the *tunica adventitia*). In arteries of small size, there is found a thin elastic membrane perforated by numerous small holes (the *fenestrated membrane* of Henle). The microscopical appearance of small vessels is seen in Figs. 78 and 79.

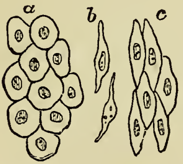


FIG. 77.—Varieties of Endothelium: *a*, from pleura; *c*, from vessels; *b*, two detached cells.

It is important to remember the following points in connection with the action of the vessels: (1) the larger arteries are highly elastic and feebly contractile; (2) the smaller arteries are highly contractile and feebly elastic; (3) the capillaries are elastic and contractile, but it is difficult to estimate the extent of their elasticity; and (4) the veins are very distensible, and are both feebly elastic and feebly contractile. Wundt gives the following figures as to the coefficient of elasticity:—

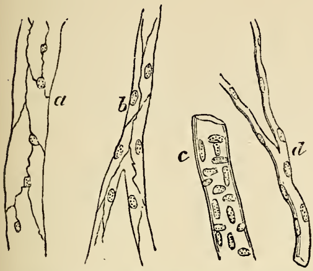


FIG. 78.—Capillaries of various size: *a*, capillary much magnified and acted on by nitrate of silver, so as to show that it is made up of flattened cells; *b*, a smaller vessel showing the same; *c*, a small artery or vein showing transverse and longitudinal nuclei; *d*, ultimate capillary from *pia mater* of sheep's brain.

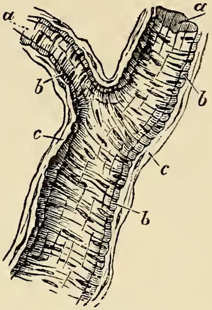


FIG. 79.—An artery of intermediate size: *a*, *a*, openings of branches and position of lining of vessel; *b*, *b*, *b*, muscular coat showing transverse nuclei; *c*, *c*, coat of connective tissue.

	Coefficient of Elasticity in Grammes.
Arteries,	72·6
Veins,	94·9
Portion of Aortic Wall,	161·0
Aorta, in longitudinal direction,	60·1
Aorta, in transverse direction,	38·1
Jugular Vein, in longitudinal direction,	97·4
Jugular Vein, in transverse direction,	47·0

As the arteries pass outwards, they give off branches, the united calibre of which is, with rare exceptions, greater than that of the parent vessel. Thus, as Küss expresses it, the arterial system may be regarded as a cone, the base of which ends in the capillaries, whilst the summit is at the aorta; on the other hand, the venous system is a second cone, the base being also at the capillaries, and the apex at the right auricle. Vierordt states that the area of the capillaries is to the area of the aorta as 800 : 1, and the area of the veins as 400 : 1. This, of course, is merely an approximation, and it may be very wide of the mark.

In studying the circulation in the vessels, we shall consider (1) the arterial, (2) the capillary, and (3) the venous, circulations. Afterwards, it will be necessary to examine the conditions which regulate arterial pressure and rapidity of current, both as regards the heart and the nervous arrangements. It will assist the student, however, in the first instance, to study, in a general manner, the laws regulating the passage of fluids through tubes.

a. *Flow of Fluids in Tubes.*

1. *Rigid Tubes.*—The movements of fluids in rigid tubes may be readily studied by connecting together pieces of glass tubing, of equal calibre, having vertical tubes, of the form of an inverted T, thus ⊥, inserted at various distances in the course of the horizontal tube. Such vertical tubes are termed *Piezometres*, and the amount of pressure exerted by the fluid in the horizontal tube may be measured by the height to which the fluid ascends in the vertical tube. When fluid is forced through such an arrangement of rigid tubing and piezometres, say 10 or 12 feet in length, by means of an elastic compression bag, it is noticed that the fluid issues from the other end in jets, each jet corresponding to a contraction of the bag when pressure is made on it. The following laws may also be illustrated :—

(1) The pressure is constant in all the points of a transverse section of the tube.

(2) The pressure diminishes regularly in the direction of the current.

(3) The pressure is increased by any obstacle placed in front of the flow of fluid—such as (*a*) elongation of the tube; and (*b*) diminution of its calibre. The pressure increases as the square of the rapidity. Thus, if the rapidity be 1, 2, 3, 4, the pressure will be 1, 4, 9, 16, &c.

(4) The *mean* rapidity is equal in all parts of the tube, and it varies: (*a*) with the *calibre* of the tube—it increases as the calibre becomes greater; (*b*) with the *length* of the tube—the shorter the tube, the greater the rapidity; (*c*) with the *pressure*—the rapidity increases as the square root of the pressure; (*d*) with the *nature of the fluid*—viscous fluids moving more slowly than limpid fluids; and (*e*) with the *temperature* of the fluid—increasing as the temperature rises with a given fluid.

(5) The volumes of the fluids discharged are proportional to the squares of the diameters of the discharging tubes.

2. *Elastic Tubes.*—When a stream of water is transmitted through a long elastic tube, formed, say, of india-rubber, the fluid does not issue from the other end in a series of jets but it flows continuously. If a finger be placed on any part of the tube, and more especially near the force-pump, an expansion and relaxation of the tube will be felt with each stroke. Further, if the right fore-finger be placed over the tube near the force-pump, and the left fore-finger on a more distant portion, a stronger impulse will be felt with the right than with the left. There is thus the transmission of a wave

along the tube, the wave diminishing in amplitude as the distance from the force-pump increases. The progress of this wave may be traced graphically by an apparatus devised by Marey, which is shown in Fig. 80.

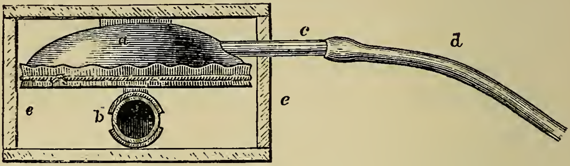


FIG. 80.—Section of apparatus for transmitting the movement of an elastic tube to a recording tambour (*Marey*): *a*, tambour, placed in a wooden box *e e*, having the membranous surface adjusted over the tube *b*; *c*, tube passing from tambour and attached to the registering tambour by the india-rubber tube *d*.

It consists of a rectangular wooden box, open at both ends, having in its interior a tambour which is carefully adjusted over the elastic tube. The slightest expansion of the tube acts on the tambour and is conveyed by the tube in connection with it to the registering tambour. By placing a series of these box-tambours at regular intervals along an elastic tube, shut at one end, and connecting each with a registering tambour, as seen in Fig. 81, the various phenomena connected with the transmission of the wave may be recorded with precision.

The experiment is conducted as follows: After adjusting all the tambours and the chronograph so that they can be brought into contact with the cylinder when it has attained its maximum velocity, a sudden impulse is given to the force-pump *c*, so as to send a wave through the elastic tube, and at the same moment, the registering tambour and the chronograph are brought into contact with the cylinder. The tambour 1 acts first, then 2, 3, and so on, each inscribing its curve on the cylinder, and time is registered by the chronograph. The result is what is seen in Fig. 82, copied from Marey.

This tracing enables us to study (1) the rapidity of the propagation of the wave; (2) the movement of the reflected wave; (3) the changes in height of the wave at different parts of its course; (4) the successive changes of form of the wave; and (5) the formation of secondary waves from a single impulse. The *rapidity* of the wave may be ascertained by measuring the time which ensues between the instant of its appearance under the first tambour, and the moment it appears under the second. Thus if we draw

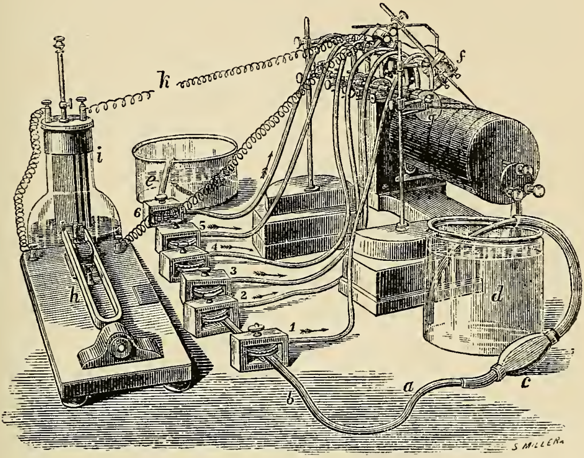


Fig. 81.—Arrangement of apparatus in the experiment for registering the movement of a wave along an elastic tube: *a b*, long elastic tube of india-rubber, passing from the vessel *d* under the tambours 1, 2, 3, 4, 5, and 6, to the vessel *e*. Force-pump seen at *c*. Each receiving tambour is connected with a registering tambour and all are adjusted to the cylinder as at *g*; *f* is the chronograph, worked by the current from the battery *i*, interrupted by the tuning fork *h*. The small arrows ⟶ indicate the direction of the impulse from the receiving to the registering tambour.

a line from the summit of each wave (see Fig. 82) down to the chronographic tracing, the rapidity may be measured

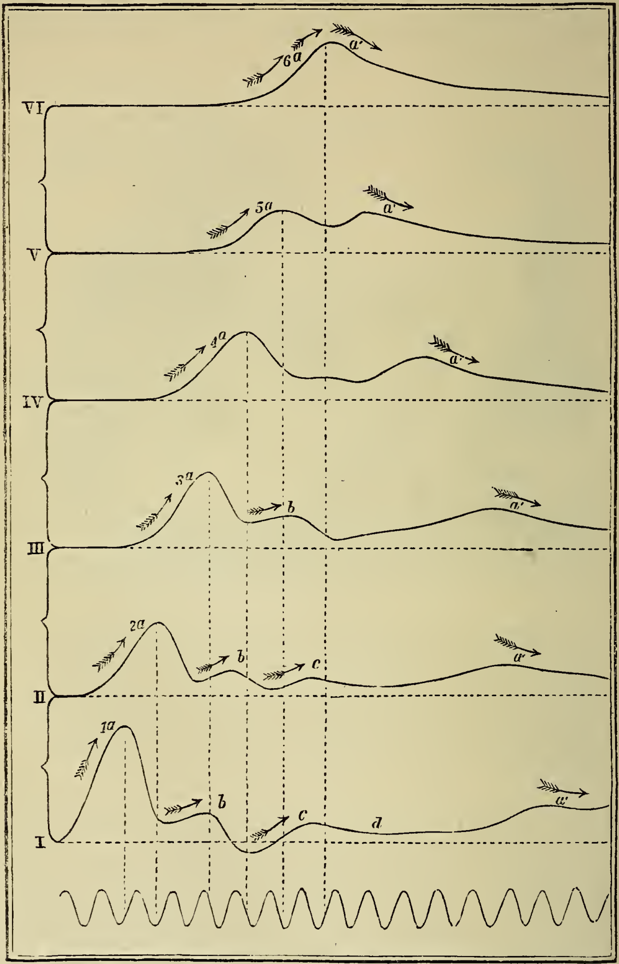


FIG. 82.—Tracings of the movements of a wave in a shut elastic tube. The length of the horizontal dotted lines I. to VI., represent time,

as registered by the chronograph = 50 vibrations per second. The tambours were placed at distances of 20 centimetres along the elastic tube, so that from I. to II., from II. to III., from III. to IV., from IV. to V., and from V. to VI., the distance is 20 centimetres. The letters *a*, *b*, *c*, *a′*, in the six superposed tracings, mark each the summit of the same wave, and thus its progress may be followed. Thus 1*a*, 2*a*, 3*a*, 4*a*, 5*a*, and 6*a*, indicate the progress of the wave *a*, and the arrows indicate the direction in which it is propagated. When the positive wave reaches the shut end of the tube, it is reflected, and the course of the reflected wave is indicated by the letters *a′* 6, *a′* 5, *a′* 4, *a′* 3, *a′* 2, and *a′*1. The secondary waves are indicated by the letters *b*, *c*, *d*; thus *b* is the second wave, *c* the third, *d* the fourth. It will be observed that these waves are much less marked; *b* does not pass beyond the third tambour, that is to say, after it has traversed a distance of 40 centimetres; while *c* does not pass beyond 20 centimetres.

with ease, and it will be found that the wave travels 20 centimetres in the $\frac{1}{50}$ of a second—that is, a velocity of about 10 metres per second. The chief point to notice with regard to the *reflected* wave is that it almost blends with the advancing wave near the shut end of the tube (see line VI., 6 *a* and *a′*, in Fig. 82), and that it is further and further distant from the advancing wave as we pass in the direction of the force-pump. It will also be seen, on studying the tracing, that the wave has two maxima, as regards amplitude, one at each end of the tube, and that the minimum is in the middle of the tube. After an exhaustive research conducted in this manner by Marey, he arrives at the following amongst other conclusions, all of which have an important bearing on the hydraulics of the circulation and on a correct theory of the phenomenon of the pulse:[1]

1. When a fluid enters intermittently and with rapidity an elastic conduit, it forms a series of *positive* waves which are transmitted with a velocity independent of the movement of translation of the fluid.
2. The *rapidity* of the transmission of a wave is proportional to the elastic force of the tube; it varies in the inverse ratio with the density of the fluid em-

---

[1] For details, see Marey's paper—Movement des Ondes Liquides in Physiologie Experimentale, 1875, p. 87.

ployed; it diminishes gradually in the progress of the wave; and it increases with the rapidity of the impulsion of the fluid.

3. The *amplitude* of the wave is proportional to the quantity of fluid which enters the tube, and to the suddenness of its entrance; it diminishes gradually during the course of the wave.
4. When the afflux of fluid in the tube is short and energetic, it may also form, with a single impulse, a series of secondary waves, according to the laws of vibratory movement.
5. When fluid enters the tube in great quantity, and for a sufficiently long time, its prolonged afflux is opposed by a retrograde oscillation which gives origin to secondary waves.
6. When fluid is propelled into two branched tubes, of similar calibres and thicknesses of walls, a very complicated mixture of waves passes from the one tube into the other. But, in the conditions of the circulation of the blood, the aorta does not permit the passage of waves from one artery into another. The aorta has its proper waves, which it transmits into all the arteries to be there transformed, more or less; but, on the other hand, the aorta acts as an elastic reservoir for all waves passing backwards from the arteries, absorbing them completely, so that the waves of each artery are peculiar to itself and are never transmitted into any other artery or arteries.
7. When a fluid is intermittently propelled through two tubes of equal lengths, the one rigid and the other elastic, more fluid will be discharged by the elastic than by the rigid tube.

b. *Arterial Circulation.*

1. *General Considerations.*—The arterial walls are at the same time muscular and elastic—the muscular coat, as already stated, predominating in the smaller, whilst the elastic coat is strong in the greater arteries. The chief action of the elasticity of the greater vessels is to transmute, in accordance with the principles already stated, the intermittent action of the ventricle into a continuous current. Thus, when the ventricle contracts, it propels a certain amount of blood into the elastic aorta which slightly expands in all directions. On the commencement of the diastole of the ventricle, the *vis-a-tergo* is removed, the semilunar valves are closed, and the aorta recoils by its elasticity so as to force part of its contents into the vessels farther onwards. These in turn, as they already contained a certain quantity of blood, expand, recover by an elastic recoil, and transmit the movement with diminished intensity. Thus, a series of movements, consisting of expansions and contractions, gradually diminishing in amplitude, pass along the arterial system, from the greater to the smaller vessels, the latter becoming less and less elastic. These expansions and relaxations of the artery constitute the *pulse.* The undulations which we term the pulse represent merely transmission of movement—a transmission which must not be confounded with the progression of the blood, as a fluid. The undulations of the pulse travel with a rapidity of 9 *metres* per second, about 30 times faster than the rapidity of the movement of the blood, which, in the carotid artery of the horse, has been estimated to be 300 *millimetres* per second.

2. *The Pulse.*—The movements of the arteries, termed the pulse, are now registered graphically by means of instru-

ments, called *sphygmographs*, of which the best is that of Marey, seen in Fig. 83.[1]

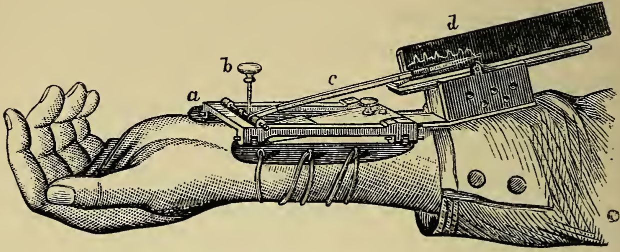


Fig. 83.—Marey's Sphygmograph in position. *a*, framework bound to the arm; *b*, screw for adjusting pressure to the vessel; *c*, lever, writing on smoked paper *d*.

It consists essentially of a long lever, which is moved near the fulcrum by a screw acting on a small horizontal wheel. The point of the screw rests on a flat disk of steel or ivory

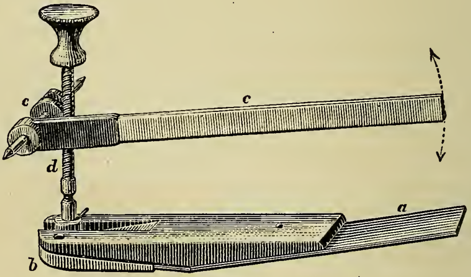


Fig. 84.—Transmitting portion of Marey's sphygmograph. *b*, ivory plate applied to the artery; *a*, steel spring; *d*, fine screw working on the wheel *c*, on the axle of which the end of the lever is fixed. The arrows represent the direction of the movements of the end of the lever, and it will be seen at a glance that this arrangement increases greatly the amplitude of the movements over the pulse.

---

[1] An excellent form of sphygmograph for transmitting movement by means of Marey's tambours has recently been invented by Mr. W. J. Fleming of Glasgow. It also has the advantage of graduating with accuracy, by weights, the pressure on the pulse.

which rests on the pulse. The lever inscribes the movements on a blackened surface, carried along by clock-work. The transmitting portion of the apparatus is represented in Fig. 84.

As already mentioned, the pulse is caused by movements of the arterial wall. In the arteries close to the heart, these movements are isochronous with the ventricular systole; but as we recede from the heart, the pulse becomes later and later in time. Thus Czermak estimated the delay as follows:—

			Seconds.
Carotid, after the cardiac pulsation,	...	...	0·087
Radial, ,, ,,	...	...	0·159
Posterior Tibial, ,,	...	...	0·193

The following changes take place in an artery when it pulsates: (1) It dilates and at the same time lengthens to a very small extent; (2) the pressure of the blood increases in the artery, and this increase is indicated by the feeling of hardness and resistance which is experienced when the artery is compressed with the finger. The general characters of the pulse are seen in the tracings obtained with the sphygmograph.

3. *Analysis of a Sphygmographic Tracing.*—The ascending line *a b*, in Fig. 85, corresponds to the distension of the artery, and the descending line, *b c d*, to its contraction; the length of the line *a d* represents the total duration of the movement, which is divided into two portions by the perpendicular line *b e*. The distance *a e*, then, measures the duration of the time of the relaxation of the artery, and *e d* the time

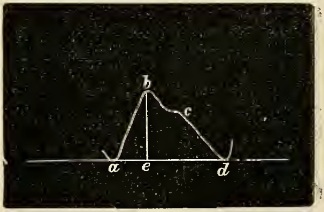


Fig. 85.—Diagram of a Sphygmographic Tracing.

of its contraction. When a continuous tracing is obtained, as in Fig. 86, it is seen that the durations of the individual pulsations are equal, and that this duration is in the inverse ratio to the number of pulsations in a unit of time. In a normal pulse, the dilatation and relaxation of the vessel succeed each other without interruption, so that there is no period of repose of the artery. When, however, the pressure of blood in the artery falls below a certain point, these characters disappear. On examining Fig. 85, it will also be observed that the duration of the relaxation of the artery is only about one-third of that of its contraction. The rapidity and the slowness of the pulse depend on the ratio of the durations of each of these periods. The pulse is quick when the duration of the arterial relaxation diminishes, and slow when this duration increases. As the line *a b* (Fig. 85) becomes less oblique and more nearly vertical, it indicates that the relaxation is short, quick, and nearly instantaneous. The line *b c d* is always more oblique than *a b*, and it usually presents a second elevation, *d*, which is more or less pronounced in different states of the pulse. Various forms of pulse-tracings are shown in Figs. 87, 88, and 89.

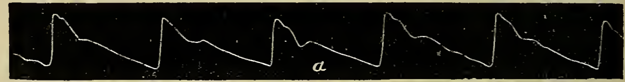


FIG. 86.—Normal tracing from radial artery.

When a pulse communicates a double impulse or beat to the finger, it is called *dicrotic*. Such is often met with in the exhaustive stages of typhoid fever and after severe hæmorrhage. Much controversy has arisen as to the exact meaning of the secondary waves seen sometimes in the descending portion of a sphygmographic tracing, and as to the explanation of dicrotism. By some it has been supposed that the second summit (*c* in Fig. 85) is due to a second impulse given to the blood in the vessel by the sudden closure of the semi-lunar valves at the opening of the aorta, and to an elastic recoil of the walls of the aorta. But such a summit may be seen in a pulse-tracing taken in a case where the aortic valves are so diseased as to be incapable of closing; and, as was pointed out by David C. MacVail, dicrotism may even be obtained by an elastic india-rubber tube without the existence of any valves. Nor can it, in the author's opinion, be due to any rebound of the blood from the minute arterioles and capillaries, as was once urged

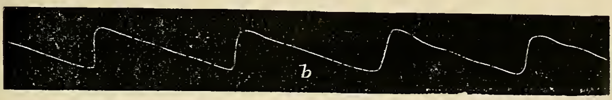


FIG. 87.—Tracing from radial artery of a healthy man. The elevation in the descending portion of the curve is scarcely observable, indicating a state of high arterial tension.

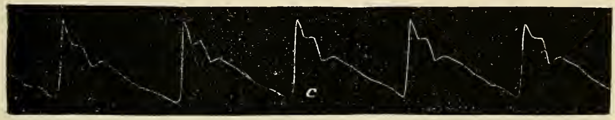


FIG. 88.—Tracing from radial artery, showing great irregularity in the descending curve, indicating by these second curves, and by the great amplitude of the principal curve, a state of low arterial tension.

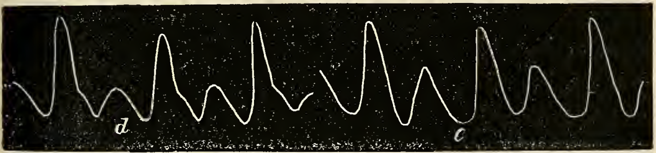


FIG. 89.—*d*, tracing of a pulse showing a smaller wave succeeding each larger wave, so that a double beat could be felt by the finger; *e*, a similar tracing, obtained in a case of typhoid fever, showing the intermediate wave still larger. Both of these tracings indicate low arterial pressure. (*Foster.*)

by Marey, as it is best marked when these are so dilated as to permit the rapid efflux of blood from them into the veins. The only remaining causes are (1) from some kind of mechanical action of the registering lever, or (2) from a periodic movement of the wall of the vessel itself. Although no doubt the form of the curve may be partially due to the inertia of the lever and of the spring, still the fact that it varies, within wide limits, with states of the circulation, would point to the periodic movement of the wall of the vessel as being the efficient cause. If, for example, the vessel be so full as to approach complete distension (high tension), and if more blood be then forced into it, the wall of the vessel will yield a little more, the pulse will be firm and hard, and the tracing obtained will be similar to Fig. 87. On the other hand, if the vessels be only partially full (low tension), it is evident that when more blood is propelled into it, distension will take place to a considerable extent, and there will be an oscillation of the wall of the vessel at that point. In these circumstances, the pulse will be soft and compressible, and the pulse-tracing will resemble Figs. 88 or 89*d* or 89*e*.[1] The three factors producing an arterial pulsation are: (1) the more or less energetic contraction of the ventricle; (2) the quantity and pressure or tension of the blood; and (3) the elastic and contractile properties of the arterial wall. If we modify any of these factors, there will be a corresponding modification in the physical characters of the pulse.

4. *Contractility of Arteries.*—Involuntary contractile fibre, as has been already stated, exists to a considerable amount in the walls of the smaller arteries, and the calibre of the

---

[1] In the author's opinion, the question of the cause of dicrotism will not be settled until tracings are obtained with a recording apparatus in which the inertia is reduced to a minimum, and in which there is no friction. This he is attempting to do by the use of Sir William Thomson's siphon recorder.

vessels may be changed by the activity of the contractile coat. The contractility of vessels may appear under two forms: (1) *rhythmical contractions,* such as have been observed in the vessels in a rabbit's ear, or in a bat's wing, which are independent both of the pulse and of respiratory movements; and (2) *persistent contractions,* under the influence of the nervous system, which play an important part in the distribution of blood. The amount of contraction of an artery will affect the pressure of the blood in its interior, it will accelerate or retard the rapidity of the blood current, and it will regulate the supply of blood to the capillary area to which the vessel is distributed. By such arrangements, also, the distribution of blood to various organs is regulated, thus establishing what has been termed a *balance of local circulations.* For example, if the vessels in one organ remain permanently contracted whilst those in a neighbouring organ are dilated, more blood will pass to the latter than to the former, and thus some end of physiological importance may be served. Thus physiological correlations may be established between the cerebral and thyroid circulations, the gastro-hepatic and the splenic circulations, and the distribution of blood in the lower extremities as related to the abdominal organs. The nervous arrangements which govern the vessels will be described after studying the phenomena of the circulation in the capillaries and in the veins.

c. *Capillary Circulation.*

The circulation in the capillaries may be readily studied by placing under the microscope any transparent membrane containing vessels, such as the web of a frog's foot, the mesentery of a frog, the lung of a toad, the tail of a fish, the wing of a bat, &c., &c. When seen under favourable conditions, the following phenomena may be noticed :—

1. In the smaller arterioles and veinules and in the capillaries, the current is continuous, and there is no pulse. By the elasticity of the larger vessels, the intermittent movement of the blood, caused by each ventricular contraction, has been transformed into a continuous flow.

2. In some of the larger vessels, the current is more rapid than in others of equal calibre, that is to say, the current is more rapid in small arteries than in small veins.

3. In the ultimate capillaries (which may be recognized by their diameter being about that of a single blood corpuscle) the current appears to have a uniform velocity in all capillaries of the same size.

4. Sometimes a slight acceleration of the rapidity, even in the smallest vessels, may be observed to follow each cardiac beat.

5. In a vessel larger than an ultimate capillary, so large as to permit the passage of several coloured corpuscles abreast, the coloured corpuscles may be seen travelling with great apparent velocity in the centre of the stream, whilst the colourless corpuscles move more slowly next the walls of the tube. It will also be observed that the coloured corpuscles remain separate from each other, and do not exhibit any tendency to adhere together, or to stick to the walls of the vessels, whereas the colourless corpuscles do both, more especially after the membrane has been exposed for some time to the air, so as to excite the early stages of inflammation.

6. If the calibre of an ultimate capillary be marked at the beginning of the observation, and again sometime afterwards, it will frequently be noticed that it has become narrower or wider, indicating that contractility is one of the physiological characteristics of capillary bloodvessels The causes which produce the change of calibre are not known, and at present are only guessed at.

It is important to note also that the arrangement of the capillaries in an organ or tissue is adapted to the functional activity of that organ or tissue. Where there is great functional activity, there is a rich plexus of capillaries, and the converse also is true. Contrast, for example, the capillary supply in cartilage with that of muscle, or the grey matter of the nerve centres with that of the white matter. But, in addition, the distribution of capillaries always corresponds to the ultimate structural arrangements of the tissue or organ. So precisely is this the case, that a good histologist is able to identify the organ from an injected preparation showing the vessels, although none of the ultimate histological elements of the organ or tissue are to be seen. In muscle, for example, the capillaries exist in the form of elongated meshes; in connective tissue, such as is found beneath the skin, in an irregular network; and in the cortical part of the kidney, where the tubes are convoluted, we find an irregular plexus; whilst in the medullary part, where the tubular arrangement is linear, we have a linear arrangement of vessels.

The movement in the capillaries is due to the force of the heart, as modified by the elasticity of the vessels (*vis a tergo*). Some have tried to show that it is largely supplemented by an attractive influence exerted by the tissues (*vis a fronte*), and the statement is supported by the fact that wherever we find an increased demand for blood, we have an increase in the amount of blood flowing to that part, such as occurs, for example, in the mammary gland during lactation, and in the growth of horn. Such an attractive influence on the part of the tissues is quite conceivable as a force assisting in the onward flow of blood; but its amount is immeasureable by any known means, and it is almost infinitesimally small in relation to the amount of blood moved, in comparison with the force exerted by the heart.

d. *Venous Circulation.*

The walls of the veins are thinner, less elastic, and more distensible than the walls of the arteries. They contain both elastic and contractile tissue, though to a smaller extent than the arteries. Rhythmic contractions have been observed in the splenic and mesenteric veins, and in the mouths of the venæ cavæ; but there does not appear to be any evidence to show that a condition of permanent contraction of veins takes place.

The circulation in the veins, as in the rest of the vascular system, depends upon (1) inequality of blood pressure; (2) on muscular action compressing the veins, and thus, in consequence of the valves found in many veins opening towards the heart, so acting on the blood as to force it onwards in the direction of that organ; (3) on the movements of respiration; and (4) the suction action of the right, and, in the case of the lungs, that of the left, auricle of the heart. All of these must have an influence on the onward flow of the blood in the veins, but the exact and relative effect of each has not been precisely determined.

The flow of blood in veins is continuous, so that, when a vein is cut, it does not spurt as happens in an artery, but it "wells" out in a stream. There is, normally, no pulse in a vein. Sometimes, however, a pulse may be observed in the veins of the neck, isochronous with the auricular systole, when there is an obstruction to the passage of blood from the auricles to the ventricles. A pulse in the veins is also possible when there is such rigidity from pathological changes in the walls of the greater vessels as to destroy the elastic influence of these parts, and, at the same time, such a degree of dilatation of the arterioles and capillaries, as to admit of the onward propulsion of the movement caused by the heart's contraction.

c. *The Pressure of the Blood in the Vessels.*

As the blood is circulating through vessels, under the influence of the action of the heart, it exerts a certain pressure or tension, the existence of which is shown by the jet of blood which is thrown out on puncturing an artery, and the amount of which is indicated by the height to which the jet is propelled. The first attempt to measure the pressure in the vessels of the living body was made in 1744, by Stephen Hales, who connected a long vertical tube, provided with a stopcock, as seen in Fig. 90, with the crural artery of a horse, turned the stopcock (or untied a ligature, which has practically the same effect), so as to admit the blood of the animal into the vertical tube, and observed the height of the column of blood and the oscillations to which it is subjected with each beat of the heart. A diagrammatic view of the tube used by Hales is shown in Fig. 90 (the left-hand figure).

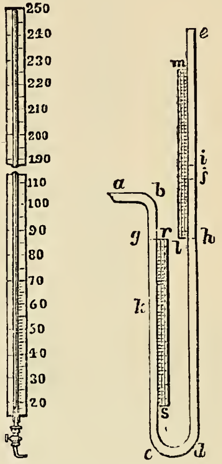


Fig. 90.—To the left, the tube used by Hales, which may be graduated to the most convenient standard, such as fractions of an inch, or millimetres. To the right, the bent tube of Poiseuille: *a*, connected with vessel, communicating pressure to mercury in bent tube, *b*, *g*, *k*, *c*, *d*, *h*, &c. The two limbs carry a graduated scale.

It is evident that by such an arrangement the pressure exerted on the vessels might be measured by the height of the column of blood, and that the variations in pressure would be indicated by the oscillations of the column. It was not until 1828, that Poiseuille bent the tube into the form of the letter U, and placed in the bend some mercury, which was at the same time more mobile and much heavier, per volume, than blood. This arrangement, seen in Fig. 90,

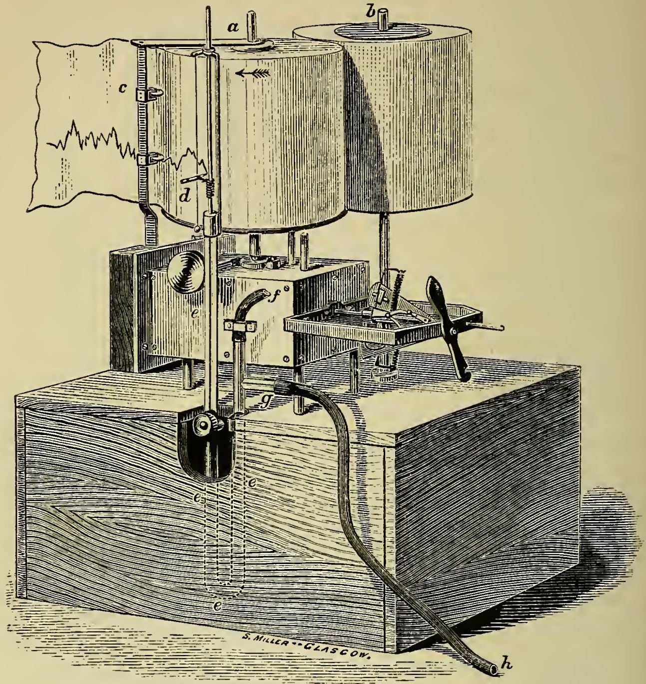


FIG. 91.—Mercurial Kymographion for recording mean blood pressure and its larger variations. *a*, band of paper rolling off, in the direction of the arrow, from the cylinder *b*; *e e e*, U-tube containing mercury, bearing on the surface of the mercury in one limb a float, to which is connected the marker *d*, inscribing the curve seen on the paper; *f*, tube for connection with a bottle of carbonate of soda, elevated above the apparatus so as to exert sufficient pressure to prevent the blood from entering, except to a very slight extent, the canula inserted into a vessel, say the carotid, and communicating with the tube *h g*. Carbonate of soda solution is used as the medium for connecting the blood with the mercury, because it prevents to a considerable extent the risk of the blood coagulating in the tube. (*Burdon-Sanderson.*)

constituted the *Hæmadynamometre* of Poiseuille. By attaching to each column of mercury a graduated scale, and connecting one limb of the tube (the shorter) with the vessel, arterial pressure was thus communicated to the mercury, the amount of which was indicated by a depression of the metal in *k* and an elevation in *h*. The next great improvement in the apparatus was made by Ludwig,[1] who made arrangements for communicating to a moving surface the oscillations of the column of mercury. This he accomplished by placing on the surface of the mercury in the longer limb a little float, carrying a marker, which recorded, on a moving surface, any oscillations of the mercury. Such an apparatus is termed a *Kymographion*, a simple form of which is seen in Fig. 91.[2]

The apparatus of Ludwig, from the inertia of the mass of mercury, can only register mean blood pressure, and the more delicate variations escape notice. Fick has attempted to register these smaller fluctuations by means of a kymograph, a simple form of which is seen in Fig. 92, consisting of a hollow spring, filled with distilled water, one end of

---

[1] The notion of communicating variations in pressure to a moving surface is generally supposed to have originated with James Watt, who contrived, by this method, to record the movements of a pressure gauge attached to a steam-engine. But it must be remembered that recording apparatus on this principle were constructed for meteorological purposes by Ons-en-Bray, in 1734; by Changeux, in 1785; and by Rutherford, in 1794.

[2] Full details as to the mode of using this instrument are given by Burdon-Sanderson in the Handbook for the Physiological Laboratory, p. 209. As there pointed out, what is recorded is not the actual movement of the artery, but the oscillations of the mercurial column, so that the curve is not that of the wall of the artery but of the manometer. It is also evident that if the column of mercury perform wide excursions, small variations, produced say by very rapid beats of the pulse, will be unnoticed. Still, although the instrument does not give absolute, but only relative, variations in pressure, it has been of great service in physiological research, more especially as relating to the influence of the nervous system on the vessels and the effect of drugs.

it being connected with the vessel, and the other, bearing a lever arrangement for inscribing the oscillations of the spring on the moving surface.

An improved form of the apparatus is used in the physiological laboratory of the University of Glasgow, and

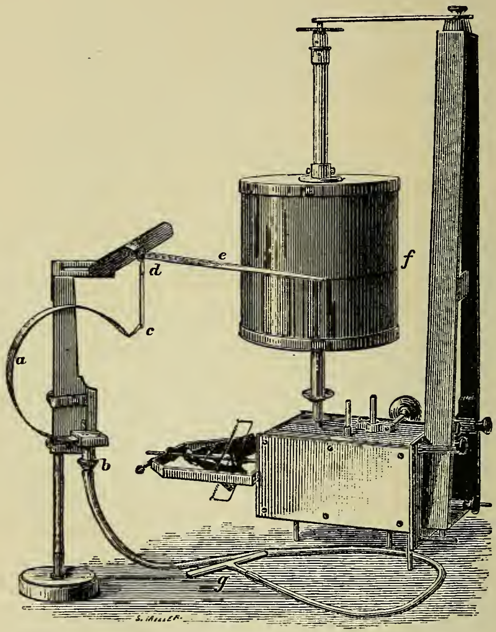


FIG. 92.—Fick's kymograph, of a simple but incomplete form. *a*, hollow spring, connected by *b* with lead tube, ending in ┬-shaped tube *g*, which is introduced into the vessel; the other end of the spring *a* is connected by *c* with the lever *d e*, which inscribes the oscillations of the spring on the cylinder *f*.

is shown in Fig. 93. It has the advantage of facility of adjustment and of recording with accuracy *a single* oscillation of the spring, which cannot be readily done with the apparatus shown in Fig. 92, in consequence of successive oscillations occurring after the first impulse.

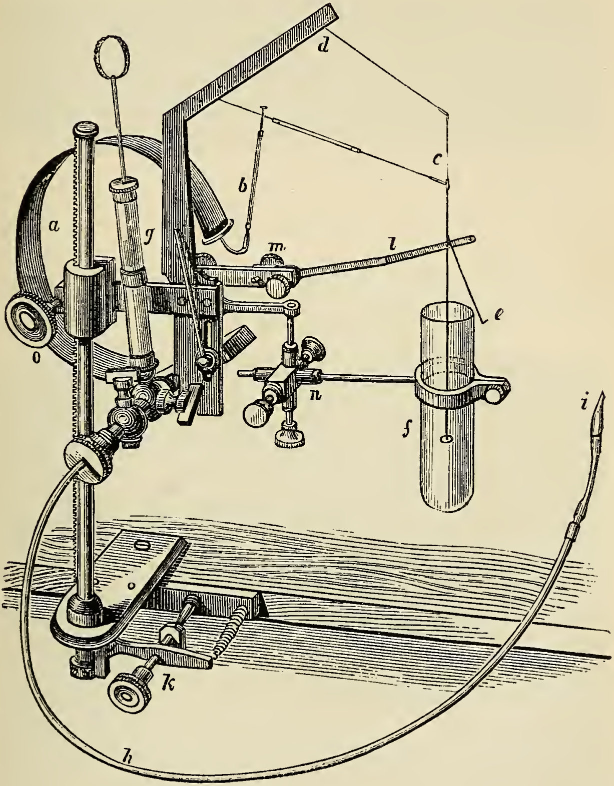


FIG. 93.—Improved form of Fick's kymograph. *a*, hollow spring, bearing lever arrangement *b d c*, to which is attached the marker *e*; the rod *c* passes downwards into the tube *f*, containing glycerine, so as to offer a certain resistance to the oscillations of *c*; *g*, syringe for filling the tube *h* with carbonate of soda, and to exert a certain pressure so as to prevent the blood from passing into the tube *h* at *i*, the canula inserted into the vessel; *l*, abscissa marker, which can be applied to the moving surface by turning the screw *m*; *k*, screw for adjusting the whole apparatus to the moving surface; *o*, screw for elevating or depressing the kymograph; *n*, screw for adjusting the position of the tube *f*.

An example of a tracing obtained by Ludwig's kymographion is shown in Fig. 94.[1]

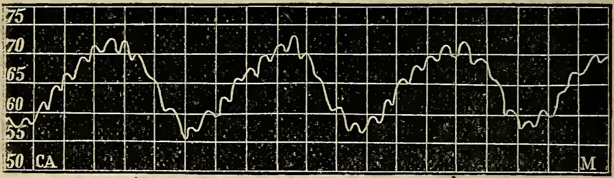


Fig. 94.—Pressure of blood in the carotid of a dog. (*Marey.*)

[1] In the Physiological Laboratory of the University of Glasgow, there is a very complete form of kymograph, made by Rudolph Rothe of Prague, from designs furnished by Professor Hering of that city. It leaves nothing to be desired in the way of mechanical arrangements, and it reduces to a minimum the labour of recording blood pressure. An example of a small portion of a tracing is here given.

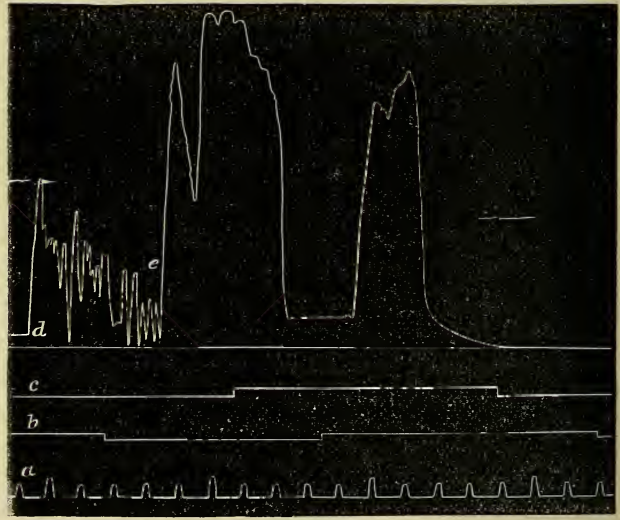


Fig. 95.—Tracings obtained with the large kymograph of Rudolph Rothe. *a*, signal of seconds made by a clock interrupting the current in an electro-magnetic recording apparatus, showing, for facility in counting, every fifth second by a higher curve than the others; *b* and *c*, lines drawn by markers in connection with electro-magnetic signalling apparatus by which the moment of stimulating a nerve, or of the occurrence of any other phenomenon may be recorded; *d*, abscissa line; *e*, oscillations of the manometer.

From Fig. 94, it will be observed that there is (1) an increase and diminution of blood pressure with each cardiac beat, as seen in the smaller curves; and (2) an increase and diminution produced by respiratory movements, the increase occurring during inspiration, and the decrease during expiration, as indicated by the larger waves. It is evident also that all the lesser curves have the same general character, and that they show nothing as regards any variation in pressure during individual beats. To show such slight variations, the kymograph of Fick must be used, when such a tracing as the following may be obtained.

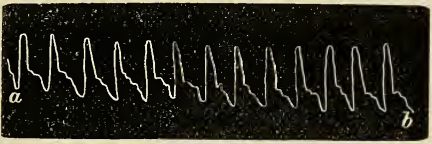


Fig. 95*a*.—Traces obtained from the dog with Fick's kymograph, by Burdon Sanderson.

Finally, to estimate pressure, Marey has used either the cardiograph (Fig. 61, p. 312), or pressure-bag introduced into the cavities of the heart, and he states that his method may detect variations which would escape notice by the others.

By such methods of research, the following conclusions have been arrived at as regards *arterial* pressure—(1) the pressure diminishes from the heart to the capillaries; (2) it attains its maximum in the ventricle at the moment of systole, and its minimum in the auricle at the moment of diastole, at which time also the pressure in the auricles and in the great veins may be negative, that is, below atmospheric pressure; (3) in the carotid of the rabbit, it amounts to from 5 to 9 centimetres of mercury, in the dog from 10 to 15, in the horse from 20 to 32, and in man it has been estimated as being about 15 centimetres of mercury; (4) the arterial pressure at any given point undergoes periodic variations—increasing at the instant of ventricular systole, and diminishing during diastole—variations which are most marked in arteries near the heart; (5) these periodic variations may be observed in the intermittent jetting of an artery when it is punctured; (6) we must distinguish between the mean arterial pressure at any point of an artery, and the mean pressure of the blood in the whole arterial system—which can only be obtained by taking the mean of the pressures in many different arteries at unequal distances from the heart; (7) the mean arterial pressure depends directly on the quantity of blood in the arterial system, and consequently on the total calibre of the system, so that any diminution of calibre, produced mechanically, or by nervous influences, will increase the mean arterial pressure; and (8) the mean arterial pressure increases with the energy of the beats of the heart.

As regards *venous pressure*, it has been ascertained (1) that in the veins near the heart the pressure is only $\frac{1}{20}$th to $\frac{1}{10}$th of that of the corresponding arteries; (2) during auricular diastole, the pressure in the veins may become negative; (3) there are no periodic variations of pressure in the veins as in the arteries, except in the great venous trunks in the neck and near the heart, where there is a diminution of pressure during auricular diastole and an increase during auricular systole; and (4) great activity of the heart diminishes venous, whilst it increases arterial, pressure. *Capillary* pressure has not, for obvious reasons, been directly measured, but we may regard it as being intermediate between the pressure in the smaller arteries and the pressure in the smaller veins. The pressure in the capillaries exercises an important influence on the transudation of liquor sanguinis, and consequently on the interchanges between the tissues and the blood.

Attempts have also been made to measure the pressure in the cavities of the heart. Chauveau and Marey (see Fig.

67, p. 317) found it to be in the horse 128 millimetres in the left ventricle, 25 in the right ventricle, and 2·5 millimetres in the right auricle. Ludwig has stated the pressure in the pulmonary artery as 10 to 30 millimetres. The general facts regarding pressure may be impressed on the understanding by the diagram in Fig. 96.

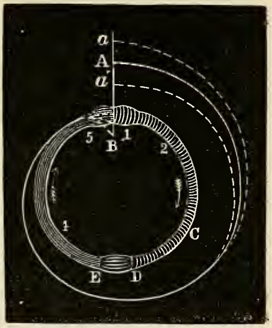


Fig. 96.—Diagram showing the pressure in the vascular system. (*Beaunis*)—1, ventricle; 2, arteries; 3, capillaries; 4, veins; and 5, auricle. From A to C, the line of pressure in the great arteries; from C to D, in the small arteries; from D to E, in the capillaries; and from E to B, in the veins. The dotted lines *a* C and *a'* C indicate the pressure during ventricular systole (*a* C) and during diastole (*a'* C). Beyond C, the blood pressure is uniform until the auricle B 5.

f. *Velocity of the Circulation.*

Various attempts have been made by Volkmann, Vierordt, Ludwig and Dogiel, Hering, and Chauveau and Lortet, to measure the velocity of the circulation, and special instruments have been invented for the purpose. Of these, the one open to fewest objections, and most likely to obtain an approximately accurate result is the *Hæmadromograph* of Chauveau and Marey, one form of which is shown in Fig. 97.

It consists of a copper tube *a*, about eight centimetres in length, which is introduced into the vessel; in the middle of the wall of this tube, there is a slit closed by an india-rubber membrane, which is traversed, as seen in 1 *a*, by a light ivory needle, one end of which floats in the fluid passing through the copper tube, whilst the other inscribes the movements on the paper *h*, moved by the clock-work *g*; the blood-current, passing through the tube *a*, moves the needle, and the movement is registered on the paper. From *a* there also passes a tube, *c*, communicating with a sphygmoscope of Marey, *b*. The *sphygmoscope* consists of a small glass cylinder, *b*, in the interior of which is a small elongated india-rubber bag communicating with the tube *c*. The sphygmoscope transmits its movements by the india-rubber tube *d* to a registering tambour, *e*, the lever of which, *f*, writes the variations of pressure in the tube *a*, alongside of the curve representing velocity. A view of the registering tambour is seen at 2 *e*. Suppose the tube *a* fixed in the carotid artery of a horse, controlled by a ligature placed above and below the apparatus. On removing the ligatures, the blood flows onwards, moves the needle in the direction of the current, and this movement, assisted by the elasticity of the india-rubber membrane through which the needle passes, is registered on the paper. The curves obtained are shown in Fig. 98.

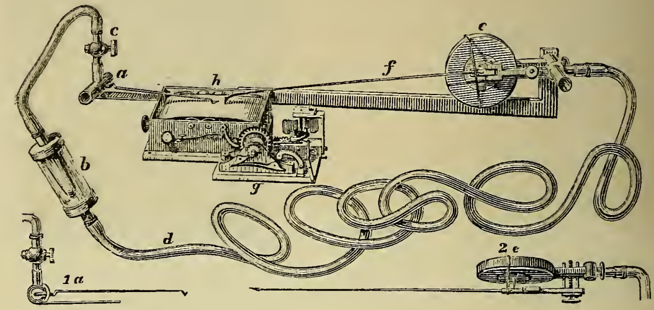


Fig. 97—Hæmadromograph of Chauveau and Lortet.[1] For description see text.

---

[1] A still more convenient form of the apparatus, as is used in Glasgow, is now made by M. Breguet, of Paris. It must be confessed that this apparatus really registers the velocity, as indicated by pressure, in a very small portion of the tube only. Ludwig has invented an instrument of a different kind, the *Stromuhr*, but it also is not free from objection.

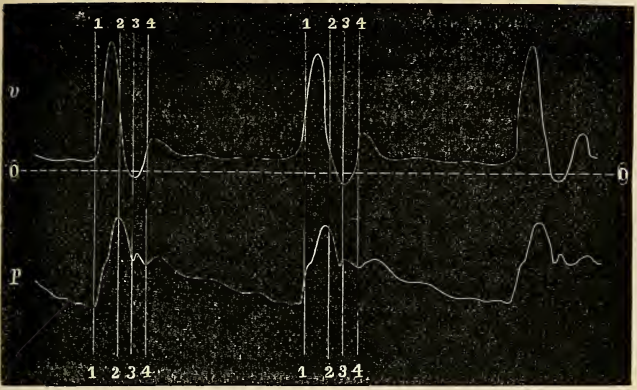


Fig. 98.—Tracings of variations of rapidity and of pressure of blood in the carotid of a horse, obtained by Chauveau and Lortet. The line *v* represents the curve of the rapidity of the blood ; and *p* the curve of arterial pressure. The figures and vertical lines represent corresponding periods in the tracings.

The following figures give, in millimetres, per second, the velocities of the blood in different parts of the vascular apparatus.

	Horse.
Carotid Artery, ...	300
Maxillary Artery, ...	165
Metatarsal Artery, ...	56
Capillaries, ...	0·5 to 0·8
Jugular Vein, ...	100 ?
Venæ Cavæ, ...	110 ?

Observe the following points : (1) the velocity of the blood is in the inverse ratio with the total calibre of the vessel—rapid in the aorta, it diminishes as we recede from it ; (2) each systole is attended by an increase in the velocity, as may be seen in the tracings of Fig. 98 ; (3) in the smaller arteries, capillaries and smaller veins, the velocity is constant and uniform ; (4) the velocity increases in the venous system as we approach the heart ; and (5) in the large veins, the movements of respiration, and probably also the suction action of the auricle during diastole causes a rhythmic increase and diminution of the velocity.

It is important to distinguish between the rapidity of the blood current and the time occupied by a blood corpuscle in making a complete circuit through the heart and vessels, say from the left ventricle to the left ventricle again. Attempts have been made to measure the time, starting from the jugular vein. Thus, Hering has injected into a jugular vein a few drops of ferrocyanide of potassium, and he has examined the blood of the opposite jugular every five seconds by testing with perchloride of iron—the formation of Prussian blue indicating the moment when the ferrocyanide made its appearance in the blood of the jugular after having made a tour of the circulation. Vierordt so modified the method as to examine the blood received every half second. The result obtained by these observers was that from 16 to 23 seconds elapsed between the time the $K_4Fe_2Cy_6$ was introduced into the right, and the moment it made its appearance in the left, jugular. In the course of these researches, Vierordt made the remarkable discovery that in most animals the rapidity of the circulation is equal to the time in which the heart makes about 27 pulsations. Consult the following table :

Name of Animal.	Weight of the body in grammes.	Pulse beats per minute.	Number of Pulsations in the duration of the circulation.
Guinea Pig, .	222	320	23·7
Cat, . . .	1312	240	26·8
Hedgehog, . .	911	189	23·8
Rabbit, . .	1434	220	28·5
Dog, . . .	9200	96	26·7
Horse, . .	380,000	55	28·8
Fowl, . . .	1332	354	30·5
Buzzard, . .	693	282	31·6
Duck, . .	1324	163	28·9
Goose, . .	2822	144	26·0

g. *Changes in the Volume of Organs caused by the Circulation of the Blood.*

It has been satisfactorily proved by various observers, and more especially by François-Franck, that there is a slight change of the volume of any distensible organ with each beat of the heart. The apparatus used by Franck is shown in Fig. 99.

By means of this apparatus, Franck has obtained numerous tracings, of which the following are a few examples—all indicating variations in the volume of the hand with each cardiac beat, and with other conditions.

These interesting observations show: (1) that the volume of an organ is not fixed, but varies according to the amount of blood contained in it; (2) that its volume changes with each cardiac pulsation, increasing when blood is forced into it, and diminishing by the emptying of the capillaries into the veins; and (3) that variations in the volume of one or more organs, say by compression, or by the application of cold, or by the internal administration of substances which affect the calibre of bloodvessels, such as ergot, will cause corresponding variations in the volume of other organs.

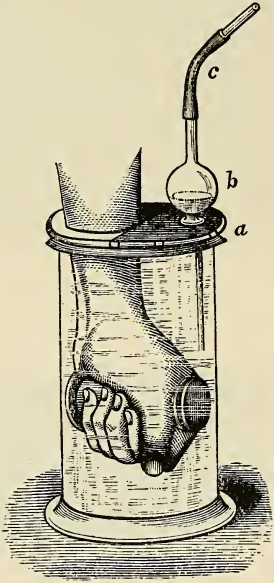


Fig. 99—Apparatus for showing changes of volume of the hand. The india-rubber membrane through which the fore-arm is passed is kept immobile by a metallic plate, *a*; a tube, blown into a bulb at *b*, is connected with a registering tambour by the tube *c*. The glass vessel is over-filled with water, the hand is inserted, and, to assist in giving steadiness, the transverse bar is firmly grasped.

They also appear to the author to have important clinical indications, but into these the limits of this work forbid him to enter.

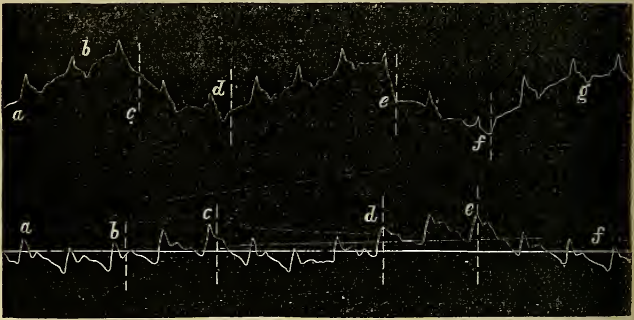


FIG. 100.—The upper line shows cardiac tracings, and the lower line shows tracings from change of volume of the hand. The two tracings were taken simultaneously. The dotted vertical lines indicate corresponding times.

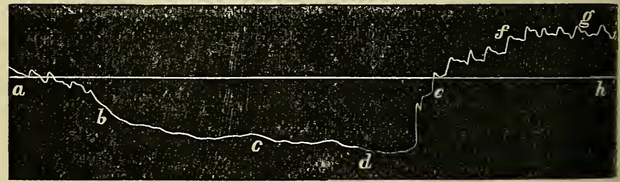


FIG. 101. Reduced tracing given by François-Franck, showing change of volume of the hand and suppression of the pulsations by compression of the brachial artery, at the time indicated by *b*. Observe the fall indicating diminution of volume and the absence of pulsations in *b*, *c*, *d*; soon after *d*, compression was removed, the curve mounted up to *e*, and oscillations recommenced.

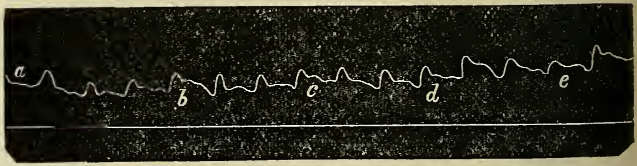


FIG. 102.—Reduced tracing given by François-Franck, showing the effect of compression of the two femoral arteries on the volume of the hand. On compressing at *b*, shortly after, at *c*, the volume of the hand increased, as shown by the ascent of the curve towards *e*.

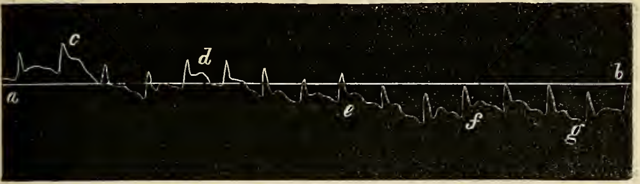


FIG. 103.—Reduced tracing given by François-Franck, showing a diminution in the volume of the hand by placing a lump of ice on the skin of the shoulder at the time indicated by *d*. Observe the falling of the curve towards *e f g*, showing diminution of the volume of the hand.

h. *The Innervation of Bloodvessels.*

In 1852, Claude Bernard made the remarkable discovery that section of the sympathetic on one side of the neck was followed by a dilatation of the vessels, and an increase of temperature, on the same side; and that electrical stimulation of the cephalic end of the nerve caused the vessels to contract and the temperature to fall. In the sympathetic, therefore, there are nerve-fibres which influence the contractile coats of the vessels. These fibres, usually called *vaso-motor*, originate in the medulla oblongata, in an area between the upper limits of that organ and the lower border of the corpora quadrigemina. In this area, consequently, there is a vaso-motor centre, from whence emanate nervous influences which tend to keep the smaller vessels in a more or less contracted condition. If this centre be injured, as has been done by Ludwig and Owsjannikow, the smaller blood vessels throughout the body dilate, they receive more blood, and consequently the pressure in the larger vessels at once falls. By connecting a kymograph with a large vessel, say the carotid, observing for a time the mean blood pressure, and afterwards injuring the supposed vaso-motor centre, Ludwig and his pupil at once observed an enormous fall of blood pressure, to be explained by the paralysis of the smaller, and a consequent rapid emptying of the larger, vessels. Having thus established the important fact of a *vaso-motor centre*, which, in certain conditions, could control the calibre of the smaller vessels, and consequently govern the distribution of blood, it was evident that this centre might in turn be arrested in its actions by inhibitory influences coming from somewhere else. This has been found to be the case. In 1866, Cyon discovered in the rabbit a nerve originating by two roots from the superior laryngeal and from the pneumogastric.[1] Stimulation of the distal end of this nerve produces no effect, but stimulation of the cephalic end causes at once a great fall of blood pressure in the arterial system, and a diminution in the frequency of the pulse. Now, it might be supposed, from what was stated at page 329, that the diminution in the frequency of the pulse was due to stimulation of the roots of the pneumogastric, but this is not the case, as the same phenomena occur after division of that nerve. Evidently, therefore, this nerve, known as the *Depressor Nerve of Cyon and Ludwig*, inhibits or restrains the activity of the vaso-motor centre.

According to Stilling, the depressor nerve does not act on the vaso-motor arrangements of the whole body, but only on those of the abdomen and lower extremities. Thus, after section of the splanchnics, which supply the vessels of the abdominal viscera, it is asserted that excitation of the depressor does not produce nearly the same diminution of pressure in the carotid vessels. Still there is a diminution, even after section of the splanchnics, a fact which appears to indicate a more general inhibitory action than Stilling allows. By this remarkable influence of the depressor, a balance is kept up between the central and the peripheric circulations. Imagine the heart to be pumping blood through the

---

[1] In many animals this nerve is blended with the pneumogastric.

vessels. If from some cause the smaller vessels become constricted, so as to offer greater resistance to the passage of the blood, the arterial pressure in the larger vessels is increased, and the heart has more work to do to overcome this resistance. If the resistance reached a certain amount, the heart would be unable to overcome it, and it would soon cease to beat. But by the influence of the depressor, this risk is prevented. At present we cannot describe the exact mechanism, but it is undoubted that an influence may pass from the heart along the fibres of the depressor to the vaso-motor centre, the effect of which is to inhibit the activity of this centre, and thus allow the smaller vessels to dilate. When this occurs either locally, as in the abdominal region, or generally, the result is a depletion of the larger vessels, a consequent fall of pressure in these, and therefore less resistance to the efforts of the heart. Thus, it would appear that in the heart itself there is an arrangement by which, to a certain extent, it governs its own work by automatic mechanisms.

Much controversy has arisen amongst physiologists as to the existence of a set of nerve filaments possessing the property of causing a dilatation instead of a contraction of the vessels. These have been termed by Schiff *vaso-dilator* nerves. Claude Bernard found that excitation of the chorda tympani (see p. 235) caused a relaxation of the vessels of the sub-maxillary gland. Erection, as occurs in the penis, has long been known to depend on dilatation of vessels and consequent increased afflux of blood. Eckhard and others have found that electrical stimulation of the nerves of the sacral plexus may produce erection, and it has been assumed that fibres in these nerves may, when stimulated, cause dilatation. Such an action is quite incomprehensible from what is known of the minute anatomical structure of vessels. These contain, as has been stated, layers of involuntary muscular fibres in the transverse and longitudinal directions, and it is difficult to understand how any contraction of fibres in either of these directions could possibly cause dilatation of the vessel. If the nerves supplying either of these sets of fibres were stimulated, there must be contraction of the fibre, and no mechanical adjustment of such contractions can cause dilatation of the vessel. It is much more probable that a kind of inhibitory action takes place. Ganglia abound in the coats of vessels. From these, fibres pass to and from the muscular elements of the vessel, and these may be regarded as local reflex centres. Such centres, however, are under the influence of two sets of fibres: (1) those which may be regarded as *accelerating*, corresponding to the fibres in the sympathetic that reinforce the activity of cardiac ganglia; and (2) those which are *inhibitory*, as, like the fibres in the pneumogastric distributed to the heart, they may restrain the activity of the local ganglia. If such be the arrangement, the observations of Eckhard and others may be explained without the necessity of assuming the existence of vaso-dilator filaments, because, in their experiments, they probably stimulated inhibitory filaments, by the action of which the local centres were arrested, and consequently there was dilatation of the vessels. There appears, therefore, to be no satisfactory evidence in favour of the view that there are vaso-dilators as well as vaso-motors. This subject will be further discussed in treating of the action of the sympathetic.

In reflecting on the relation between the vascular system, more especially as regards the calibre of arteries, the activity of the heart, and the influence of the nervous system, the following summary, modified from the statement made by Beaunis, will be found useful.

(a) *Contraction of arteries may arise from*—

(1) An excitation of vaso-motor centres; in this case, the contraction is muscular and active, and will be accompanied by an increase of blood pressure.

(2) A diminution of cardiac activity; in this case, the contraction is passive, elastic, and is not followed by any marked increase of blood pressure.

(b) *Dilatation of arteries may arise from*—

(1) A vaso-motor paralysis, either arising from strong irritation of the vaso-motor centre, as by the influence of poisons or in the course of some diseases (death during acute rheumatism), or from indirect influence of such nerves as the depressor or other sensory nerves.

(2) An increase in cardiac activity. In both of these cases (1 and 2) the dilatation is passive, and is accompanied, in the first case, by a diminution, and, in the second, by an increase, of pressure.

Consult HARVEY, Exercitationes Anatomicæ de Motu Cordis, 1628; HALES, Hæmostatics, 1744; POISEUILLE, Recherches sur la Force du Cœur aortique, 1828; VOLKMAN, Die Hæmodynamik, 1850; VIERORDT, Die Lehre vom Arterienpuls, 1855; CHAUVEAU, Nouvelle Recherches expérimentales sur les Mouvements et les Bruits normaux du Cœur, Gazette Médicale de Paris, 1856; MAREY, Physiologie Médicale de la Circulation, 1863; also Du Mouvement dans les Fonctions de la Vie, 1868; also Physiologie expérimentale, 1876, 1877; L. LORTET, Recherches sur la Vitesse du Cours du Sang, 1867; LUDWIG and DOGIEL, Die Ausmessung der Strömenden Blutvolumina, im Ludwig's Arbeiten, 1868; LANDOIS, Die Lehre vom Arterienpuls, 1872; GARROD, On the Sphygmograph, Journal of Anatomy and Physiology, 1872; BURDON-SANDERSON, On the Circulation of the Blood, in Handbook for the Physiological Laboratory, p. 208; RUTHERFORD, Lectures in the "Lancet," 1871; ANDREW BUCHANAN, The Forces which carry on the Circulation of the Blood, 1874;

Lauder Brunton, Experimental Investigation on the Action of Medicines, Part I., Circulation, 1875; Details as to Experimental Methods, and drawings of apparatus, in Cyon's Methodik der Physiologischen Experimente, 1876.

IV.—RESPIRATION.

It has already been pointed out that the presence of oxygen is essential to the life of every tissue, and that one of the products formed during vital activity is carbonic acid, a gas which is inimical to life. Such is also true with reference to the life even of humble organisms, as the amæba and infusoria. Deprived of oxygen, or introduced into a medium containing an excess of carbonic acid, they die, so that it seems to be essential to their existence that carbonic acid be removed and fresh oxygen be introduced. In all grades of animal life, an interchange between the gases of the organism and the gases of the medium in which it lives is constantly taking place, and this interchange is *respiration*. In a humble organism, small in bulk and simple in structure, no complicated mechanism is necessary, inasmuch as the body of the organism is either bathed directly by the fluid in which it lives, or there are canals, as in a sponge, passing through it in various directions, for the conveyance of the fluid, so as to bring it into intimate relation with the whole mass. When the organism increases in size and in complexity, and when a nutrient fluid is required to circulate through it, arrangements are produced, by which gaseous interchanges take place between this fluid and the surrounding medium. Thus, in the air-tubes which are distributed through the bodies of insects, and in the gills of fishes, the nutrient fluid or blood is brought into close relation with the air, and interchanges take place which constitute respiration. Still higher in the scale, we find, as in reptiles, sac-like organs differentiated, communicating with the air by means of a tube or tubes, and on the walls of which the vessels containing the blood form a network, and thus again we have facilities for gaseous interchanges between the gases of the blood and of the air in the sacs. Such sacs are the simplest form of lungs. In higher animals, the bag or lung becomes more and more complicated until it forms a honeycomb structure, the cells of which contain air. On the walls of these minute cells, capillary vessels ramify, and thus there is an enormous surface, having the blood of the organism on the one side, and the air in the lung-cells on the other, through which gases pass from the one medium to the other medium. On taking a comparative view of the process throughout the animal kingdom, it will also be observed that, in the simpler arrangements, no mechanism is necessary for facilitating the gaseous interchange. The amæba, for example, is surrounded by a fluid containing gases in solution; in higher forms, canals, along which air would pass by diffusion, seem to be necessary; in still higher forms, as in the fish, by the rhythmic movements of the gills, the water is permitted to bathe the respiratory apparatus on all sides; still higher, as in frogs, the air is forced into the air-bag by a process resembling that of deglutition; and lastly, in the highest forms, we find an automatic mechanism, involving many periodic nervous and muscular movements, by which the air is introduced into, and expelled from, the respiratory organ.

It will thus be seen that the lower organisms respire directly by changes between the body and the medium; whereas, in the higher organisms, respiration may be regarded as a twofold process: (1) *internal respiration*, or the interchanges between the gases of the blood and the tissues; and (2) *external respiration*, or the interchanges between the gases of the blood and the gases in the air-cells of the lung. Even in the higher animals, however, interchanges may take place in other regions than in the lungs. Thus, there is a true *cutaneous respiration* in the skin, an *intestinal* respiration in the bowel, and probably interchanges take place in other organs.

A.—GENERAL ANATOMICAL ARRANGEMENTS.

1. Structure of the Lungs.

If we trace the trachea downwards, we find it dividing into two bronchial tubes passing to the lungs. In the substance of the lung, each tube divides and subdivides into narrower tubes, which give off branches, and become smaller and smaller until we reach the ultimate tubes, which end in a group of air-cells. This kind of arrangement is roughly represented in Figs. 104 and 105.

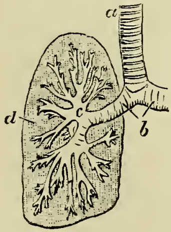


Fig. 104.—Diagram showing *a*, trachea; *b*, division of trachea into two *bronchi*; *c*, still smaller bronchi; *d*, substance of the lung.

Fig. 105.—Ultimate group of lobules of the lung. *b*, bronchial tube, dividing and subdividing; *c*, external view of group of air-cells; *d*, internal view of the same.

The trachea and bronchial tubes are lined by ciliated, but the ultimate air-cells are lined by squamous epithelium.

2. Vascular Arrangements of the Lungs.

The lung has two sets of afferent and two sets of efferent bloodvessels. The *afferent* vessels are the bronchial artery and the pulmonary artery, the first carrying arterial blood from the aorta for the nourishment of the tissue of the lung and of the walls of its tubes and vessels, and the second conveying venous blood from the right ventricle to the lungs. The *efferent* vessels, on the other hand, are the bronchial veins, carrying back blood from the lung tissue, and the pulmonary veins, returning to the left auricle the blood which has been rendered arterial by its passage through the capillaries covering the walls of the pulmonary air-cells. The tissue of the lung is also richly supplied with lymphatics, and with nerves derived from the sympathetic and from the pneumogastric.

B. MECHANISM OF RESPIRATION.

1. General Character of the Movements.

The respiratory movements consist of rhythmic changes of volume of the thorax, produced partly by the contractions and relaxations of certain muscles, and partly by the elasticity of the structures involved. As the cavity of the thorax, containing, and completely filled by, the lungs, heart, and other organs, is an air-tight cavity, and as the lungs are hollow and distensile organs lodged in this cavity, and communicating with the external air by the bronchial tubes and trachea, it is evident that any increase in volume of the thoracic cavity must be followed by an expansion, and any diminution in volume by a contraction, of the lungs. This will be clearly understood by studying the following diagram of an apparatus devised by Funke, of which various forms may be used :—

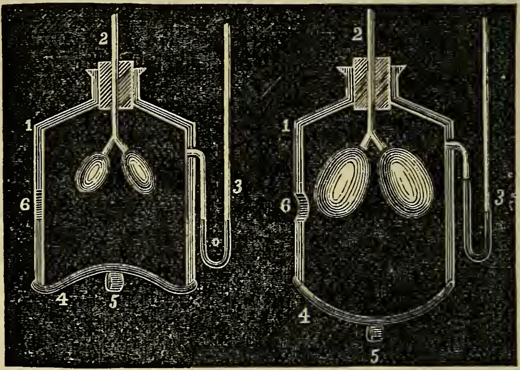


FIG. 106.—Diagrammatic view of apparatus to show the relations between the thoracic wall and the lungs. For description see the text.

Imagine a wide glass flask, 1, the bottom of which, 4, is made of strong india-rubber, having in the centre a wooden knob or cork, by which the membrane may be pushed upwards or pulled downwards at pleasure. A tightly-fitting cork is inserted into the neck of the flask, through which passes a glass tube, 2, dividing into two branches in the flask, and to the end of each tube a small india-rubber bag is attached. A mercurial manometer, 3, is inserted into an opening on one side of the flask, and an opening on the other side, 6, is covered by an india-rubber membrane. Suppose the membrane, 4, to be in the position shown in the figure on the left hand, the pressures on the inner and outer surfaces of the flask are equal, and consequently the mercury in the two limbs of the manometer is at the same level, and the india-rubber bags are collapsed. If, then, the cavity of the flask be increased, as in the right hand figure, by pulling down the membrane, 4, by the knob, 5, the pressure in the interior of the flask is diminished, and the india-rubber bags expand, the mercury rises in the shorter limb of the manometer, and the membrane, as at 6, is pressed inwards, by the atmospheric pressure, acting on 3, 2, and 6, being in excess of the pressure in the flask. When the membrane passes upwards, equilibrium of pressure is again established, as seen in the figure to the left. Imagine, further, that the capacity of the flask were increased, not only vertically, by the movement of the membrane, 4, but laterally and antero-posteriorly, by an expansion of the wall of the cavity, we would have an increase of capacity in every direction, and consequently the atmospheric pressure exerted through the tube, 2, would cause the bags to expand to a still greater extent. In the mechanism of respiration this is what really happens. By the action of the respiratory muscles, the capacity of the chest is enlarged in every direction; there is thus an excess of atmospheric pressure over the pressure on the outer surface of the lungs, and consequently a certain amount of air rushes into the air passages of the lungs, until equilibrium is again established. Ordinary inspiration is, therefore, essentially a muscular act. When the muscles relax, in ordinary expiration, the elasticity of the lungs and of the thoracic wall causes these organs to recoil to their former position, and thus to force out a certain amount of air. Thus, ordinary expiration is not muscular, but is due to the elasticity of the structures involved. Any proof that the mechanism is of the nature just described is scarcely needed, but it is offered by what occurs when a puncture is made through the thoracic wall into the pleural cavity. When this occurs on one side, there is collapse of the lung on that side and great difficulty in breathing; but if made on both sides, both lungs collapse, and there is rapid asphyxia—the cause being that although the capacity of the chest be increased as before, the lungs do not likewise expand, as the atmospheric pressure exerted on their surface, through the hole in the thoracic wall, is of course equal to that in the respiratory passages.

2. MUSCULAR ARRANGEMENTS.

The next question is, by what muscular action is the capacity of the chest increased?[1]

1. *In ordinary Inspiration.* The *vertical* diameter of the chest is increased by the contraction, and consequent descent of the diaphragm, which is the chief inspiratory muscle. The lateral parts, corresponding to the bases of the lungs, descend to a much greater extent than the central tendon, which is related on its superior surface to the pericardium and the heart. At the same time, the *antero-posterior* and *lateral* diameters are increased by the elevation of the ribs by the external intercostals, and by the portion of the internal intercostals found between the costal cartilages. The ribs are not only elevated, but slightly rotated, so that their lower borders are directed outwards, and at the same time the sternum is carried forwards. The levatores costarum and serratus posticus superior, passing from the spine to the ribs, also assist in elevating the latter.

2. In *forced inspiration*, the capacity of the chest is further increased by all the muscles which tend to fix the first rib, and thus allow the intercostals to contract with greater effect, or which act directly on the ribs from a fixed point,

---

[1] Full details are given regarding this point in all anatomical works; and the mechanism can only be fully understood by the student studying carefully the attachments and the direction of the fibres of the various muscles involved. Much controversy has arisen on various points, more especially as to the action of the intercostal muscles. All that is attempted here is to state the general facts as shortly as possible.

such as the shoulder. Thus, such muscles as the scaleni, the sterno-cleido-mastoid, the serratus magnus, the pectoralis major and pectoralis minor, and the trapezius act as inspiratory muscles when deep, forced inspirations are made.

3. In *ordinary expiration*, the elastic recoil of the walls of the chest and of the lungs, following the relaxation of the inspiratory muscles, is quite sufficient to expel the air; but in *forced expirations* the ascent of the diaphragm is assisted by the contraction of the abdominal muscles compressing the viscera, and thus forcing up the floor of the chest. This action is assisted by all muscles which depress the ribs, such as the greater part of the internal intercostals, the serratus posticus inferior, quadratus lumborum, and the triangularis sterni.

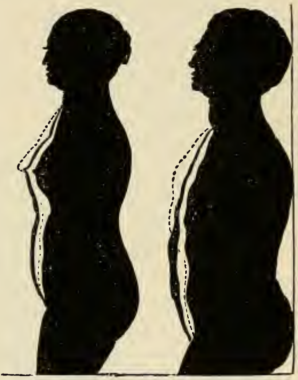


FIG. 107.—Diagrams (by Hutchinson) showing the extent of antero-posterior movement in ordinary, and in forced respiration in male and female. The back is supposed to be fixed, in order to throw forward the movement as much as possible. The black line indicates, by its two margins, the limits of *ordinary inspiration* and *expiration.* In *forced inspiration* the body comes up to the dotted line, while in *forced expiration* it recedes to the smallest space indicated. The abdominal character of respiration in the male is distinctly shown.

3. VARIETIES OF RESPIRATORY MOVEMENTS.

When the action of the diaphragm predominates, as in the male, respiration is said to be *abdominal*, or *diaphragmatic*, the abdominal wall moves upwards and downwards, and there is only a very slight increase in the antero-posterior, or transverse diameter of the chest. On the other hand, in the female, the capacity of the chest is increased chiefly by movements of the ribs, and especially of the upper ribs, causing heaving of the breast, the action of the diaphragm, and consequent movement of the abdominal wall, being much less than in man. Sometimes, in cases where a large tumour exists in the abdominal cavity, respiratory movements occur chiefly in the clavicular region. The foregoing figure by Hutchinson illustrates these forms of respiratory movement (Fig. 107).

4. REGISTRATION OF RESPIRATORY MOVEMENTS AND FORCES.

Various instruments have been invented for recording the *movements* of the thorax, by Scot Alison, Sibson, Ransome, and MacVail. The most elaborate researches on the subject have been made by Ransome, who has shown that variations in the antero-posterior diameter of the upper part of the chest are very extensive—the ends of the upper ribs moving horizontally forwards to a distance of from 12 to 30 milli-

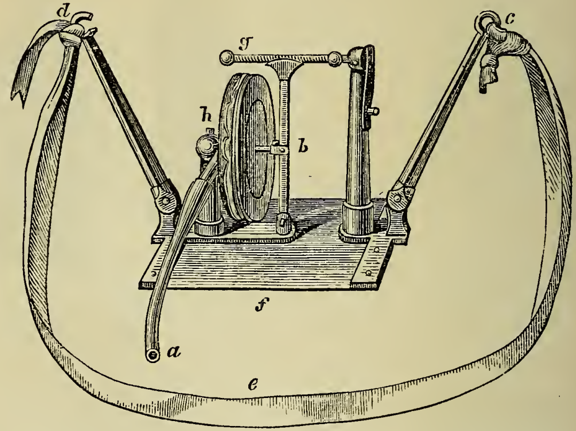


FIG. 108.—Pneumograph of Marey. *f*, very thin brass plate bearing a tambour, *h*, the aluminium disc of which is connected with the upright *b*, the upper end of which moves on a horizontal screw, *g*. The band *c e d* is placed round the body During expansion of the chest, tension occurs between *c* and *d*, which acts on the tambour by the bending of the brass plate *f*, and the movement is communicated to a recording tambour by *a*.

metres. A simple form of recording apparatus is the *Pneumograph* of Marey, seen in Fig. 108.

The apparatus is seen applied to the chest in Fig. 109, a cardiograph being used at the same time, and the two tracings, taken simultaneously with a sphygmographic tracing, are shown in Fig. 110.

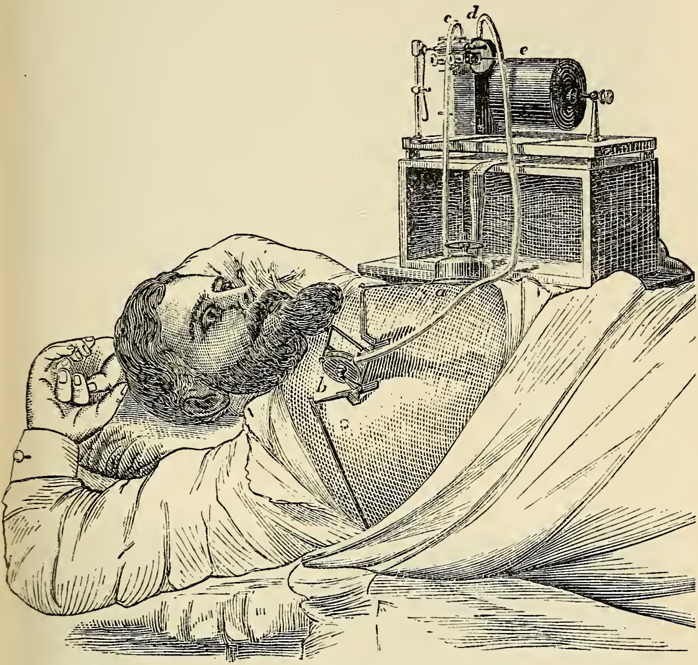


FIG. 109.—Pneumograph and cardiograph applied simultaneously. *a*, cardiograph; *b*, pneumograph.

The *elasticity* of the lungs in ordinary respiration has been estimated by means of a manometer to be from 6 to 8 millimetres of mercury, but in deep and prolonged inspirations it may amount to 30 or 40 millimetres.

The *contractility* of the lungs, which is comparatively small, and due chiefly to the muscular fibres of the bronchi, has been recorded by Paul Bert. A copy of the tracings obtained is shown in Fig. 111.

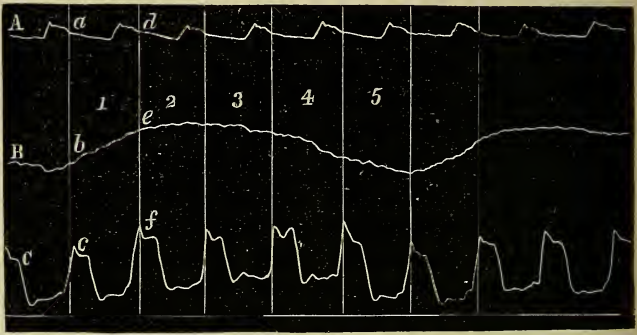


Fig. 110.—Simultaneous tracings taken by the pneumograph B, cardiograph C, and sphygmograph A at the radial artery. The ascent of the curve in B corresponds to expiration, and the descent to inspiration. There are from four to five cardiac pulsations to each complete respiratory movement. Observe also that the pulsation at the wrist is a little later than the corresponding cardiac pulsation—thus *d*, in upper line A, corresponds to *c* in lower line C.

Fig. 111.—Tracings of pulmonary contraction obtained by Paul Bert from the dog. The two upper lines were obtained by direct galvanic stimulation of the lung, and the third by stimulation of the pneumogastric. *a b c* indicate the moments of stimulation.

These tracings are important not only as affording direct proof of the contractility of the lung, but as showing that it may be excited by stimulation of the pneumogastric.

Attempts have also been made to measure and calculate the *force* exerted by the inspiratory muscles, but it must be admitted that only rough approximations have yet been obtained. These muscles must overcome the following resistances: (1) the elasticity of the thorax, the value of which has not been ascertained; (2) the elasticity of the pulmonary tissue, which, as already stated, amounts to 8 millimetres of mercury in calm inspirations, and say 24 in deep inspirations; and (3) the pressure of the air in the lungs in inspiration, say 1 millimetre in calm, and 57 millimetres in deep, inspiration. Thus the inspiratory muscles have at least to overcome resistances represented by 8 + 1 = 9 millimetres in calm, and 24 + 57 = 81 millimetres in deep, inspiration. In forced expiration, as in loud speech, crying, or making a strong expulsive effort during severe muscular action, the force must overcome a resistance equal to the positive pressure in the lung in expiration, less the elasticity of the lung, or 87 − 24 = 63 millimetres of mercury. (*Donders and Beaunis.*)

5. RHYTHM AND NUMBER OF RESPIRATORY MOVEMENTS.

Each respiratory act consists of three periods: (1) a period of inspiration; (2) a period of expiration; and (3) a period in which there is no movement, usually termed the pause. Inspiration is usually shorter than expiration, and the pause may be long or short, its duration being apparently regulated by habit or by the amount of attention directed to it. If attention be directed to respiratory movements, they become more rapid, chiefly by diminution of the time of the pause, whereas the pause becomes much longer during sleep, unconsciousness, or even when the mind is in a state of abstraction. In health, there are usually 15 respirations per minute in the adult. The following table by Quételet shows the effect of age.

AGE.	NUMBER OF RESPIRATIONS PER MINUTE.		
	Maximum.	Minimum.	Mean.
Newly-born child,	70	23	44
1— 5 years,	32	20	26
15—20 ,,	24	16	20
20—25 ,,	24	14	18
25—30 ,,	21	15	16
30—50 ,,	23	11	18

In very aged people, the number may fall even to 12 per minute. The ratio of cardiac to pulmonary movements is seen in the curve, Fig. 110; it is usually as 1 : 4 or 4·5.

6. RESPIRATORY SOUNDS.

If a stethoscope be placed over the larynx and trachea of a healthy man, two sounds will be heard—one inspiratory, and the other expiratory. These are called the *laryngeal and tracheal sounds.* If it be placed a little to the right or to the left of the manubrium of the sternum, the same sounds will be heard, but diminished in intensity. These are the *bronchial* sounds. If now we listen on either side of the chest, or on the back, over the posterior tube of either lung, two gentle rustling sounds are heard, termed the *vesicular respiratory murmurs.* All of these sounds become exaggerated during forced respiration, but in a state of health they never lose their soft character. They are produced by the passage of air through the trachea, larger bronchial tubes, finer bronchial tubes, and air-cells of the lung. Again, if we listen in the same places whilst the individual speaks, there is a peculiar resonance of the voice noticeable over the trachea: it has been called *pectoriloquy*, as if the voice entered the ear directly from the chest; over the bronchial tubes, *bronchophony*, as if the voice issued from a tube; whilst in the regions occupied by lung tissue, voice sounds are scarcely audible. The student ought to listen to these sounds in a healthy chest, so as to be able to appreciate the changes in intensity and quality of these normal sounds, and to detect the new sounds produced by pathological changes in the lung, which are of so much importance in the diagnosis of pulmonary affections.

C.—CHANGES IN THE AIR DURING RESPIRATION.

1. Mode of Examination.

Lavoisier was the first to examine, by accurate scientific methods and with skilfully-contrived apparatus, the differences between the air of inspiration and that of expiration. His method, much improved by Régnault and Reiset,

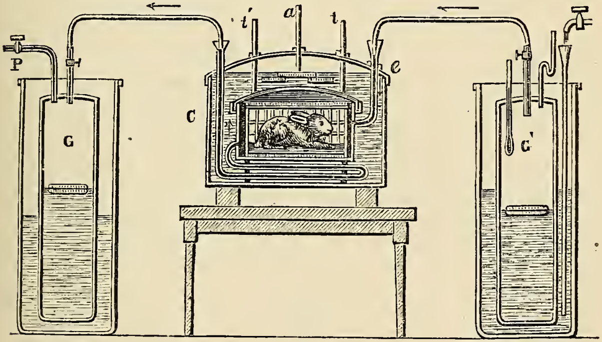


Fig. 112.—Apparatus of Dulong for the study of respiration and of animal heat. c, calorimeter, consisting of a vessel of cold water, in which the chamber containing the animal is placed; G′, gasometer from which air is expelled by a stream of water. The air enters the respiratory chamber; G, gasometer which receives the gases expired; *t t′*, thermometer; *a*, a wheel for agitating the water in the calorimeter.

consists essentially of studying the changes produced by the respiration of a small animal placed in a chamber of limited size. A measured quantity of air, freed from carbonic acid and aqueous vapour, is introduced in a continuous stream into the chamber, and passes from it through tubes containing solutions by which the carbonic acid and aqueous vapour formed by the animal are absorbed. Thus, the amount of oxygen lost, and the amount of carbonic acid and aqueous vapour gained, by the air may be accurately measured. Pettenkofer of Munich and Angus Smith of Manchester have employed chambers large enough to contain a man for several hours. A small apparatus suitable for estimating not only the amount of O used and of CO_2 produced, but the amount of heat given off from the body of the animal, is shown in Fig. 112. This arrangement will be again referred to in treating of animal heat.

2. The Air Inspired.

About half a litre, or 500 cubic centimetres, of air are taken into the lungs in each inspiration; there are 15 inspirations per minute, therefore ·5 litre × 15 × 60 = 450 litres per hour, or 450 × 24 = 10,800 litres in 24 hours.

The composition of atmospheric air, in 100 parts, is as follows:—

	By volume.		By weight.
Oxygen, . . .	20·8	……	23
Nitrogen, . . .	79·2	……	77

Carbonic acid, in pure air, usually exists to the extent of 4 volumes in 10,000 volumes. The amount of aqueous vapour depends on the temperature, being great when the temperature is high and small when it is low. Sometimes the air may be saturated with aqueous vapour at a given temperature; if the temperature rise, more vapour may be taken up; if it fall, some moisture will be deposited. In addition, air may contain dust, products of the decomposition of organic matter, ammonia, &c., &c. The temperature and the pressure of the air have an influence on respiration. If the *temperature* be high, a rarefied air is breathed—that is, an air which per volume contains less oxygen than a condensed air. Consequently, to compensate for the expansion of the air by heat, the number and depth of the respirations are increased. The *barometrical pressure*, at the level of the sea, is 760 millimetres of mercury. It is important to note the partial pressure of each gas in the air. Thus—

$$\text{The pressure of the oxygen} = \frac{760 \times 20{\cdot}8}{100} = 158 \quad \text{millimetres.}$$

$$\text{The pressure of the nitrogen} = \frac{760 \times 79{\cdot}2}{100} = 601 \quad \text{,,}$$

$$\text{The pressure of the carbonic acid} = \frac{760 \times {\cdot}0005}{100} = 0{\cdot}38 \quad \text{,,}$$

$$\text{Total barometrical pressure, . . } \underline{\underline{759{\cdot}38 \text{ millimetres.}}}$$

3. The Air Expired.

Contrast the percentage composition of the air inspired and the air expired as follows:—

	Air inspired.		Air expired.
Oxygen, . . .	20·8	......	15·4
Nitrogen, . . .	79·2	......	79·3
Carbonic acid, . .	0	......	4·3

Note the following characters of expired air: (1) it contains less oxygen; (2) it contains more carbonic acid; (3) it contains one-tenth per cent. more nitrogen; (4) it is saturated with aqueous vapour; and (5) it may contain traces of ammonia and of volatile substances. The temperature of expired air is usually about 36° C. (about 97° F.); the volume of expired air is about equal to that of inspired air, in consequence of the expansion of the expired air by increase of temperature; but if the two volumes, inspired and expired, be reduced to the same temperature and pressure, the expired air will be found to be a little less than that of inspired air, as 99 : 100, and it has been ascertained that this is due to a disappearance of oxygen. In other words, the whole of the oxygen introduced is not accounted for by what is expelled in CO_2 and H_2O, and therefore some of it is retained by the blood or tissues.

4. The Capacity of the Lungs.

The amount of air which may pass into or issue from the lungs, or which they may contain after the fullest expiration or after the fullest inspiration, may be approximately measured by means of instruments called *spirometers.* The most common is Hutchinson's spirometer, constructed on the principle of an ordinary gasometer for the storage of gas. Another is that of Casella, on the principle of the anemometer used by meteorologists for registering the velocity of the wind. A third and very convenient form, called the *anapnograph,* devised by Bergeon and Kastus, is shown in Fig. 113.

A valve, or mobile plate of aluminium, V, forms one side of a rectangular box put into communication by A with a respiratory tube terminated by a mouth- or nose-piece. The axis of rotation of the valve carries a very light lever, S, which writes on a strip of paper moved by clockwork. If air be propelled through the tube into A with each movement of inspiration and expiration, the variations of the pressure of the air in the air passages are transmitted to the valve which, by the lever, inscribes on the paper. The instrument has been graduated so as to suit bands of paper divided into small squares, each square representing a certain amount of air. Thus the instrument registers not only the pressure of the air, but the quantity inspired and expired, and the rapidity of the current of air. With such instruments, it may be shown that when the lungs have been emptied as much as possible of air by the most powerful expiratory effort, they still contain a quantity over which we have no control, and which may be estimated at about 100 cubic inches. This has been termed *residual air*. In addition to this residual air, there are about 100 cubic inches constituting *supplemental air*, or the air that remains in the chest after an ordinary expiration, in addition to the residual air already mentioned. Thus there are 200 cubic inches of air in the chest after a gentle expiration. If, then, inspiration take place gently, from 25 to 30 cubic inches are introduced; these, constituting *tidal air*, are expelled by the next expiration. We find, therefore, that in ordinary respiration there are about 200 cubic inches in the lungs, and an inward and outward current of say 30 cubic inches; but, finally, it is possible, by a very deep and

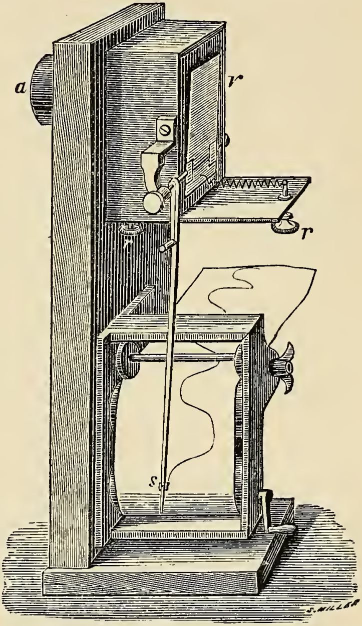


Fig. 113.—Anapnograph of Bergeon and Kastus. For description, see text.

prolonged inspiration, to introduce 100 cubic inches more. This last quantity is called *complemental air*. After the deepest inspiration, there are therefore in the lungs 330 cubic inches of air, which number expresses the *maximum capacity* of the chest. These facts may be impressed on the memory by the following table, in which both English and metrical measures are given, the English measurements by Hutchinson, and the metrical by Gréhant.

		Cub. cent.	Cub. in.		
Maximum volume of air in the lungs, 4970 cubic centimetres, or 330 cubic inches.	Residual air, . .	1200	100	Pulmonary capacity, 2800 cub. cent., or 200 cub. in.	
	Supplemental air,	1600	100		Vital capacity, 3700 cub. cent., or 230 cub. in.
	Tidal air, . . .	500	30		
	Complemental air,	1600	100		

By *vital capacity* is meant the quantity of air expired or inspired in the strongest possible respiration. The vital capacity is somewhat less in women than in men; it increases up to 35 years, and afterwards diminishes. It also increases with the height and with the circumference of the chest: for each additional centimetre in height, there is an increase of about 60 cubic centimetres. Edward Smith also showed that movement increased the volume of air expired.

5. COMPOSITION OF THE AIR IN THE BRONCHIA AND LUNG CELLS.

Having considered the composition of the air inspired and expired, and the volumes of each, it is important to ascertain what is known regarding the condition of the air in the passages and in the ultimate air-cells of the lung. It has been shown by Vierordt that as we penetrate into the lung, the proportion of carbonic acid and of aqueous vapour increases, and that if we divide the air of expiration into successive portions, the first expired contains less CO_2 than the second, the second than the third, and so on. It is difficult to estimate the percentage amount of CO_2 in the ultimate air-cells, but it is certainly not less than from 7 to 8 per cent. After an inspiration, introducing, let us say, 500 cubic centimetres of air, the air passes only into the trachea and upper air passages, driving backwards and compressing the air in the lungs at the end of the previous expiration. Diffusion then quickly takes place, oxygen passing inwards and carbonic acid passing outwards. In the next expiration, 500 c.c. are returned, but of these, as has been ascertained by Gréhant, 170 c.c. consist of pure air which was introduced by the previous inspiration, and the remaining 330 c.c. consist of vitiated air returned from the lungs. The 330 c.c. of pure air not returned diffuse quickly with the air in the deeper passages of the lungs, and Gréhant has stated that this will probably take place in the time occupied by about five respirations.

6. PARTIAL PRESSURES OF THE AIR IN THE AIR-CELLS.

Suppose the shorter limb of a manometer to be connected by a tube with the trachea of an animal, during inspiration the mercury would rise in the shorter limb, and during expiration it would rise in the longer limb—that is, during inspiration the pressure in the air passages is less than the pressure of the air, and during expiration it is greater. This amount has been found to be—

In calm inspiration, ...	− 1	mm.
In deep inspiration, ...	− 57	,,
In calm expiration, ...	+ 2 to 3	,,
In forcible expiration, ...	+ 87	,,

From these data, it is easy to calculate the partial pressures of the gases in the two states.[1]

The great difficulty is to state precisely the partial pressures of the gases in the ultimate air-cells. This is attempted as follows by Beaunis:—

		Oxygen.			Carbonic Acid.	
		Percentage.	Partial Pressure in mm. of Mercury.		Percentage.	Partial Pressure in mm. of Mercury.
Inspiration.	Calm,	17	129	...	4	30
	Deep,	20	140	...	1	7
Expiration.	Calm,	16	121	...	5	38
	Deep,	13	110	...	8	67

The above table is to be thus read: After a calm inspiration, the pressure of O in the ultimate air-cells = 129 mm. of mercury, or the pressure which would be exerted by a gaseous mixture containing 17 per cent. of O at the same temperature.

Having now studied the mechanism by which the air is introduced into the lungs, so as to reach the air-cells, let us next consider the condition of the blood before and after it passes through the lungs, so that we may be in a position to understand the conditions of the gaseous interchanges occurring in these organs.

---

[1] Thus: Let P = partial pressure, H the pressure of the air inspired or expired, and Q the quantity of gas in 100 volumes—

$$P = \frac{H \times Q}{100}.$$

Suppose H = 760 mm. and Q 20·8, then $\frac{760 \times 20\cdot 8}{100} = 158$.

	Pressure of Air.		Partial Pressure in MM. of Mercury.		
			Of O.		Of CO_2.
Inspiration.	Calm, 760 − 1 = 759	...	157	...	·37
	Deep, 760 − 57 = 703	...	146	...	·07
Expiration.	Calm, 760 + 2 = 762	...	117	...	31·5
	Deep, 762 + 87 = 849	...	130	...	36·4

D.—CHANGES IN THE BLOOD DURING RESPIRATION.

1. GENERAL STATEMENT.

The blood which reaches the lungs by the pulmonary artery is *venous,* whilst that carried back to the heart by the pulmonary veins is *arterial.* Arterial blood is of a rich vermillion colour, it coagulates readily, and it contains more oxygen and less carbonic acid than venous blood; venous blood is of a purple colour, and it contains more carbonic acid and less oxygen than arterial blood. The following table shows the percentage of gases in the two kinds of blood:—

	Arterial Blood.		Venous Blood.
Oxygen, . . .	20	......	10
Carbonic acid, . .	50	......	60
Nitrogen, . . .	2	......	2

It is not easy to estimate the gases of the blood in the pulmonary capillaries; but such blood may be supposed to be identical with that of the right ventricle. If so, it would appear that the gases in the venous blood of the right heart are—oxygen, 9 per cent.; carbonic acid, 35 per cent.; and nitrogen, 2 per cent.; and it will be observed that the amounts are smaller than those given for ordinary arterial and venous blood. Certain substances in blood have a strong chemical affinity for the oxygen or carbonic acid of respiration. Thus, hæmoglobine, as described in p. 295, unites readily with oxygen to form $\underline{\underline{\mathrm{H}}}\mathrm{O}$, 1 gramme of $\underline{\underline{\mathrm{H}}}$ absorbing 1·2 to 1·3 cubic centimetres of O at 0° C. and 1 metre of pressure. The phosphate and carbonate of soda in the plasma appear to form some kind of loose chemical combination with carbonic acid.

Another point to be observed is the quantity of blood which passes through the lung at a given time. With each systole, the right ventricle propels into the lung 180 grammes of venous blood, so that in each respiration there passes four times that quantity—180 × 4 = 720 grammes, which contain about 245 c.c. of CO_2 and 63 c.c. of O. When these 720 grammes are arterialized, they contain 210 c.c. of CO_2 and 105 c.c. of O. If these figures be near approximations, 35 c.c. of CO_2 have been eliminated and 42 c.c. of O have been absorbed. It is probable that these figures are too high, and that they might be reduced by about one-third, as analyses of expired air show, in the same time, only 21 c.c. of CO_2 and 27 c.c. of O. The chief source of error is likely due to admitting that the right ventricle sends to the lung so much as 720 grammes of blood during each complete respiratory act.

2. EXTENT OF THE RESPIRATORY SURFACE.

When we consider on the one hand the apparently small bulk of the lungs, and on the other the amount of gaseous interchange just stated, it is evident that the anatomical arrangements of the lung must be such as to admit of an enormously-extended surface. Küss has made an attempt to estimate the extent of this surface. Supposing the number of air-cells to be from 17 to 18 millions, the surface will be about 200 square metres. Of this surface, about three-fourths, or 150 square metres, are occupied with capillaries; so that a blood-surface of 150 square metres is brought into juxtaposition with an air-surface of 200 square metres. No doubt these figures are merely approximative, and there may exist an error of even 20 per cent., but they help the mind in forming some conception of the conditions, as regards surface, in which gaseous interchanges occur.

3. Pressure of the Gases in the Blood.

If a gas be dissolved in a fluid, it exists in a certain state of tension or pressure. Let the pressure be increased, at the same temperature, the fluid may be caused to take up more gas; on the other hand, let the pressure be diminished, the gas will escape, until an equilibrium is again established. The gases in the blood, however, are not all simply in a state of solution: they are partly dissolved and partly in a state of loose combination with certain elements of the blood, most of the oxygen being united to hæmoglobine. Pflüger and Strassburg have estimated the pressure in the blood of the dog, and given the following figures :—

	Tension of O in mm. of Mercury.	Tension of CO_2 in mm. of Mercury.	Percentage of O.	Percentage of CO_2.
Arterial, .	29·2	21	3·9	2·8
Venous, .	22·0	41	2·9	5·4

That is to say, the arterial blood of the dog will absorb no oxygen when exposed to an atmosphere containing 3·9 per cent. of that gas, and the venous blood will give off no CO_2 into an atmosphere in which 5·4 of CO_2 already exist.

E.—GASEOUS INTERCHANGES BETWEEN THE BLOOD AND THE AIR IN THE PULMONARY CELLS.

We now come to the most difficult problem in the physiology of respiration. An organic membrane, consisting of the walls of the air-cells and of the walls of the capillaries, has on the one side of it a mixture of various gases, oxygen, carbonic acid, and nitrogen in a certain state of tension, and on the other a fluid in which the gases, oxygen, and carbonic acid are partly dissolved according to the law of pressures, and partly in a state of loose combination with certain elements of the blood—the problem is to define precisely the physical conditions in which oxygen passes into the vessels from the air-cells, and carbonic acid passes out from the blood. It is evidently complicated by our ignorance of the exact conditions as regards pressure which would affect the O in the state of $\underline{\text{H}}$O, and the CO_2 in combination with the soda salts of the blood. The following table contrasts the conditions, the arrows indicating the direction in which one would expect diffusion to take place. The assumption is made that the pressures of the gases in the blood of man are considerably greater than the figures given on the preceding page regarding the gases in the venous blood of the dog, as it is known that CO_2 in human pulmonary air-cells is above 5·4 per cent., and may be so high as 10·8 per cent. If so, with the pressure represented by this percentage, it would be impossible to understand how CO_2 could possibly escape from the blood. Thus:

	Tension of O in mm. of Mercury.	Tension of CO_2 in mm. of Mercury.
Venous Blood, ...	40	80
Organic Septum, ...	↑	↓
Air in Pulmonary Cells, . .	129	38

Thus it will be seen that the law of diffusion, under different tensions, explains both the absorption of O and the elimination of CO_2.

a. *The Absorption of* O.

It has been estimated that about 700 grammes of O are required in twenty-four hours. It is absorbed partly as the result of the chemical affinity of $\underline{\text{H}}$ and partly as an effect of pressure. The absorption of O occurs both in inspiration and in expiration. It is increased by movement and by cold.

b. *The Elimination of* CO_2.

About 900 grammes of CO_2 are eliminated in twenty-four hours. It would appear that its separation from the blood occurs chiefly during inspiration, by which fresh air is quickly introduced into the air-cells, thus lowering pressure. Any lowering of pressure or diminution of the density of the external medium favours the separation of CO_2. Deep inspirations increase it, but if pulmonary ventilation be interfered with or arrested, the CO_2 accumulates in the air-cells and a state of equilibrium may so soon be brought about which will prevent the exit of any more CO_2. Dewar and the author ascertained that the inhalation of ozone prevented the elimination of CO_2, and as the density of ozone is greater than that of CO_2 ($16 \times 3 = 48 \div 2 = 24 : 12 + 32 = 44 \div 2 = 22$), it is probable that the greater density of the ozone was the explanation of the fact. Numerous researches have shown that various circumstances affect the elimination of CO_2, of which the following are the chief:—

(1) *Number of Respirations.*—By increasing the number of respirations, keeping their depth as far as possible the same, the amount of CO_2 eliminated is increased.

(2) *Depth of Respirations.*—Keeping the number the same, and increasing the depth, the amount is increased.

(3) *Length of the Respiratory Pause.*—If the time of the respiratory pause be increased, the amount of CO_2 separated is greater, indicating that the elimination of CO_2 from the blood into the air-cells is going on even during the pause.

(4) *Age.*—The amount of CO_2 exhaled increases until thirty years of age, and afterward diminishes. This must be chiefly due to less CO_2 being formed after thirty, in consequence of less rapid changes of tissue which might produce it. It cannot be said that sex has any marked effect.

Sometimes it is stated that the difference between the amount of CO_2 exhaled by men as contrasted with women is much greater, but the difference depends not on sex, but on the nature of the occupation and on the amount of muscular exertion.

(5) *Food.*—The nature of the food, as has been shown by the laborious observations of Edward Smith, has a marked effect. The amount of CO_2 increases with the carbon contained in the food, hydrocarbons and vegetable acids yielding more than fats and albuminates. Starvation, or a state of hybernation, diminishes the amount of CO_2.

(6) *Muscular Action.*—This increases the amount of CO_2, as has been ascertained by researches conducted by Pettenkofer, Voit, Parkes, &c., and is what might have been expected, as it is well known that muscular activity cannot take place without the production of CO_2.

(7) *Sleep.*—During this condition the amount of CO_2 is diminished. It has been estimated that for 100 parts of CO_2 eliminated in 24 hours, 58 parts are separated during the day, and 42 parts during the night. Pettenkofer and Voit observed that, during a day of rest, a man eliminated 533 grammes of CO_2 during the twelve hours of day, and 395 during the night; whilst, during a day of work, he eliminated 856 during the day, and 353 during the night, thus showing that during the night following a day of hard work there was a great increase in the amount of CO_2 thrown off, even taking into account the increase during the day.

c. *Elimination of Nitrogen.*

As already stated, the air expired always contains a little more nitrogen than the air inspired. From 7 to 8 grammes are thus eliminated daily, which may be derived partly from the nitrogen of the food, and partly from the nitrogen contained in the air introduced into the alimentary canal along with the food.

d. *Elimination of Aqueous Vapour.*

About 300 grammes of aqueous vapour are eliminated by the lungs daily. This amount is derived from two sources, (1) the water of the blood, and (2) the water contained in the air previously inspired. The amount of water separated from the blood will depend on the hygrometric state of the air inspired, and upon the depth of the respirations. The absolute amount of watery vapour separated by the lungs increases with the depth and duration of the respirations: whilst cold, a low barometrical pressure, and dryness of the air, produce the same effect.

e. *Respiration in a Confined Space.*

If an animal be placed in a confined space, where the renewal of air is impossible, the air loses by degrees its oxygen, and becomes more and more highly charged with carbonic acid. When the proportion of oxygen does not fall below 15 per cent., respiration is normal; from 15 to 7 per cent., respiration becomes deep and prolonged; from 7 to 4½ per cent., respiration is carried on with great difficulty; and below this amount, there is risk of immediate asphyxia. After death, the blood is still found to contain some oxygen, and the tissues continue to absorb the oxygen of the blood for some time. The rapidity of asphyxia will depend on the quantity of oxygen in the confined space. Thus a ligature applied tightly round the trachea, by diminishing the space containing oxygen, produces almost immediate asphyxia. It is important to observe that when an animal is placed in a confined space, there appears to be a kind of tolerance gradually established, by which it will live in an atmosphere fatal to another of the same species introduced directly from without. Thus, Claude Bernard placed a bird under a bell-glass over mercury; three hours afterwards, he introduced another bird into the same space; the second bird died in convulsions in a few minutes, while the first continued to respire.

But, as already stated, not only is the oxygen removed, but the percentage of carbonic acid increases. Other gases and volatile substances, such as carburetted hydrogen, sulphuretted hydrogen, volatile fatty acids, &c., are also separated from the body. These latter give to the air the peculiar odour and "stuffy" character observed in crowded apartments. The object of ventilation is not only to introduce fresh oxygen, but to dilute the carbonic acid and matters just mentioned to their normal amount. Pure air contains of CO_2 about ·4 volumes in 1,000. It has been ascertained that air containing one volume per 1,000 of CO_2 has a sensible odour, and may be regarded as impure, and it has been established as a principle in ventilation that the amount of CO_2 present ought never to pass ·7 per 1,000. About 12 litres of CO_2 are expired in an hour; to dilute this to the proportion of ·7 of CO_2 per 1,000, about 18,000 litres of air free from CO_2 are required per hour. But as ordinary air contains ·4 per 1,000 of CO_2, it is evident that more than 18,000 are required. Pettenkofer, who is a renowned authority on such a subject, gives the amount at 22,000 litres, or 60 cubic metres of air—that is, about 1800 cubic feet of air ought to be supplied per head per hour in efficient ventilation. It is evident that even a larger quantity is necessary in the wards of hospitals and in sleeping apartments. The practical problem in ventilation is to supply this amount of air by such arrangements as secure freedom from cold and draughts.

F.—ABNORMAL RESPIRATION.

There are three forms of what may be regarded as abnornal respiration, namely, Apnœa, Dyspnœa, and Asphyxia.

1. APNŒA.

When the blood is saturated with oxygen, respiratory movements are arrested. This may be observed during the process of performing artificial respiration by means of bellows, or other appliances, as requires frequently to be done in the course of physiological research. If the interval between the successive insufflations be gradually diminished, the respiratory movements become slower and may even be altogether arrested, whilst other movements, as those of the heart and reflex actions, continue.

2. DYSPNŒA.

By this term is meant difficulty in breathing, which may arise either from (1) puncture of the pleural cavity preventing expansion of the lungs, as already explained (p. 377), or (2) obstruction in the air passages preventing the free passage of air to and from the lungs. It may also be caused by any conditions of the lung, such as congestion, pneumonia, tubercular solidification, &c., which diminish the extent of respiratory surface. Dyspnœa is characterized by increased respiratory movements, in which numerous muscles take part. Thus, in addition to the ordinary respiratory muscles such as the diaphragm, other muscles, such as the scaleni and posterior serrati, take part. The ribs are forcibly elevated and depressed; and the larynx, which is almost motionless in ordinary respiration, is drawn upwards and downwards through a considerable distance.

3. ASPHYXIA.

This is the state produced by interruption of the respiratory process so as to lead to the accumulation of CO_2 in the blood. It may come on gradually, as when an animal is placed in a confined space, or suddenly as by complete occlusion of the trachea. In either case, it may be divided into three stages: (*a*) *First stage.*—This is characterized by dyspnœa or difficulty in breathing. The respiratory movements are hurried and somewhat irregular; the expiratory muscles contract powerfully, and the muscles, especially of the thoracic and abdominal regions, contract spasmodically. At the end of about one minute, the spasmodic movements extend more or less to the muscles of the extremities, chiefly affecting the flexors. (*b*) *Second stage.*—The convulsions cease and the movements of expiration are scarcely perceptible; the pupils are dilated; the eyelids do not shut on touching the eyeball; reflex movements cease; the muscles become loose or flaccid; the arterial pressure falls very low; and there is a state of calmness which presents a striking contrast to what was observed a minute before. The second stage also lasts about one minute. (*c*) *Third stage.*—The ordinary inspiratory muscles act more feebly and at longer intervals of time; whilst the accessory inspiratory muscles occasionally contract spasmodically, so as to produce a series of convulsive gasps; similar convulsive movements now and then occur in the muscles of the extremities, more especially in the extensors, the head is bent backwards, and the body may also be arched in the same direction; the nostrils are dilated; and after one or two convulsive movements, death ensues. On examining the body, the venous system generally, the right cavities of the heart, and the capillaries of the lungs are found to be full of blood, whilst the arterial system is nearly empty.

The phenomena of asphyxia produced by slow degrees are essentially the same and consist of the three stages of convulsive expiratory movements, calm, and convulsive inspiratory movements.

G.—INNERVATION OF RESPIRATION.

The nervous arrangements of respiration consist (1) of a respiratory *centre* or centres in the medulla oblongata and upper part of the spinal cord; (2) of filaments of the *pneumogastric* distributed to the lungs; and (3) of the various nerves distributed to the muscles of inspiration and expiration, constituting what has been long known as the *respiratory system of Charles Bell.*

1. Respiratory Centres.

The whole of the encephalon, with the exception of the medulla oblongata, may be removed from an animal without destroying the mechanism of respiration. It will also continue in these circumstances even after removal of the spinal cord from below the origin of the phrenic nerves. These observations, first made by Legallois and Flourens, fixed the site of the respiratory centre in the medulla. The latter observer asserted that it was located in a particular part of the medulla, namely, at the lower end of the calamus scriptorius, inasmuch as he found that puncture of this part at once arrested the movements and caused death. Recent observations by Prokop Rokitansky indicate that the centre is not exclusively at this region. By increasing the reflex sensibility of other parts of the cord by means of strychnia, Rokitansky found that even the portion termed by Flourens the *nœud vital,* or vital knot, might be removed without stopping the respiratory movements. The conclusion therefore is that the centre is situated in the medulla and upper part of the cord.

2. Influence of the Pneumogastric.

Our knowledge of the importance of this nerve upon respiration has been obtained by experiment. It has been found that excitation of the trunk of the pneumogastric in the neck accelerates respiratory movements and increases the depth of respiration; whilst excitation of the superior laryngeal nerve, the filaments of which give sensitiveness to the mucous membrane of the larynx, slows the respiratory movements and lessens the depth of respiration. The same results may be obtained on dividing the nerves and stimulating their cephalic ends, but the effects vary according to the strength of the stimulus employed. Thus, by increasing the excitation of the cephalic end of the pneumogastric, the inspiratory muscles become strongly affected, so as to cause deep long-drawn respirations, and if the excitation be still slightly increased, a tetanic state of the inspiratory muscles ensues and respiration is arrested. It is evident, therefore, that the pulmonary part of the pneumogastric contains fibres which are related by reflex arrangements with the *inspiratory muscles*. On the other hand, feeble excitation of the superior laryngeal is followed by a flaccid or paralytic state of the diaphragm, whilst strong excitation causes contraction of the expiratory muscles, and if very strong, there may be arrest of respiration with tetanus of the expiratory muscles. It follows, therefore, that the filaments of the superior laryngeal exercise a paralyzing influence over the inspiratory, and an exciting influence, by reflex arrangements, over the *expiratory muscles*. It has also been observed that section of the pneumogastric, below the point where the superior laryngeal branch is given off, is followed by slowing of the respiratory movements, a fact which may be explained by remembering that the section has cut off the pulmonary exciting fibres from the centre, and left the paralysing fibres in the superior laryngeal intact. It is evident also that such a section, by severing the filaments of the inferior or recurrent laryngeal, will paralyse the muscles of the larynx, and thus interfere with the passage of air into the lung.

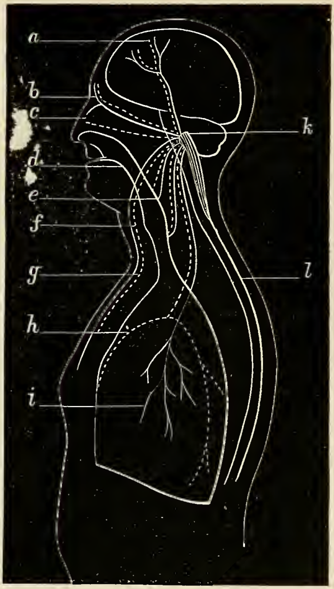


Fig. 114.—Diagram showing the position of respiratory centre, and the afferent nerves which influence it (*Lauder Brunton*). Inspiratory nerves are indicated by plain, and expiratory, by dotted lines.

a, Inspiratory and expiratory Fibres for voluntary alterations in respiration.
b, Cutaneous Nerves of face.
c, Nasal branch of fifth.
d, Superior Laryngeal.
e, Inferior Laryngeal.
g, Cutaneous Nerves of Chest.
Chiefly expiratory
f, Larynx.
h, Expiratory fibres of Vagus excited by distension of the lung.
i, Inspiratory fibres of Vagus excited by collapse of the lung.
k, Respiratory centre in medulla and cord.
l, Spinal cord.

3. THE RESPIRATORY SYSTEM OF BELL.

The respiratory centre may be excited to action by influences transmitted from the periphery of the body along the general sensory nerves. Thus we may excite a powerful inspiratory effort by dashing cold water on the face, or by a current of cold air directed on the surface of the body. The motor or efferent fibres are those which Sir Charles Bell grouped together in his "respiratory system." The most important of these are the phrenics which supply the diaphragm, the intercostals, the facial, and the spinal accessory, which sends motor filaments to the pneumogastric.

The foregoing diagram will assist the student in studying the nervous arrangements of respiration (Fig. 114).

4. INFLUENCE OF THE BLOOD ON THE RESPIRATORY CENTRES.

It has been ascertained that the respiratory centre may be directly influenced by the gases of the blood. Thus, when the blood contains an excess of carbonic acid, violent inspiratory movements take place (*dyspnœa*); and when on the contrary the blood contains only a small amount of carbonic acid and an excess of oxygen, the respiratory movements are also arrested (*apnœa*). Traube has shown that if we attempt to carry on respiration with pure hydrogen instead of atmospheric air, and if at the same time the carbonic acid be removed, the hydrogen replaces the oxygen of the blood but dyspnœa does not occur. In like manner, when by compression of the carotids, fresh arterial blood is prevented from reaching the brain, there are general convulsions; and it has been observed that at the moment when the course of the blood is re-established, there is a marked increase in the desire to breathe. These facts clearly show that the accumulation of CO_2 in the blood acts directly as an excitant of the respiratory centre. Probably also the CO_2 in the blood of the pulmonary capillaries acts upon the ends of the nervous filaments which then transmit an impression to the respiratory centre. In addition to CO_2, other active substances, such as nicotine, stimulate the respiratory centre. Increased temperature of the circulating blood has also been found to have the same effect.

5. RECAPITULATION.

The following table, modified from that given by Lauder Brunton, will show the principal ways by which respiratory movements may be accelerated or retarded.

The respiratory movements may be accelerated by—	1. Stimulation of nerves.	*a.* Stimulation of the vagus.
		b. Action of a voluntary centre in the cerebrum.
		c. Strong irritation of cutaneous nerves, as by douche of cold water, current of air, &c.
	2. Increased action of respiratory centre.	*a.* Increased temperature of the blood as in fever.
		b. Increase of CO_2 in the blood as in asphyxia.
		c. By the action of drugs—as nicotine.
The respiratory movements may be rendered slow by—	1. Diminished action of respiratory centre.	*a.* Diminution of CO_2 and increase of O in the blood.
		b. Action of drugs, such as morphia.
	2. Stimulation of nerves.	*a.* Slight irritation of cutaneous nerves.
		b. Action of voluntary centre in the cerebrum.
		c. Paralysis of the vagi, as by section.
		d. Irritation of superior laryngeal nerve.
		e. Irritation of inferior laryngeal nerve.
		f. Irritation of nasal nerves.

6. ANOMALOUS RESPIRATORY MOVEMENTS.

Such movements as cough, sneezing, laughing, moaning, &c., may be explained by a disturbance of the equilibrium between the exciting and paralysing arrangements of the respiratory nervous mechanism. Thus, in *coughing*, usually arising from an irritation in the laryngeal passage, the paralysing effect of the sensory filaments of the larynx reaches a certain intensity, there is then a deep inspiration, which is followed by a sudden and strong expiration in consequence of a transformation having taken place from a paralysing into an exciting effect. *Sneezing* is produced in an analogous manner, but the irritation commences in the nasal passages. The other respiratory movements, such as laughing, groaning, sighing, yawning, &c., which frequently originate in psychical states, seem chiefly to be associated with movements of the diaphragm. Thus, in laughing, there is a short inspiration, then a pause, and afterwards a rapid series of expiratory efforts; in groaning or blowing the nose, the expiratory effort is much more prolonged; and in sighing and yawning the inspiratory and expiratory efforts are both prolonged and of about equal length.

As already mentioned, gaseous exchanges between the blood and surrounding atmosphere take place in the skin, but these will be discussed in treating of that organ. In the meantime it is sufficient to state that from 500 to 800 grammes of aqueous vapour, and from 1 to 2 grammes of carbonic acid are thus separated.

With reference to respiratory movements, consult HUTCHINSON, Art. Thorax in Cyclopædia of Anat. and Physiology: VIERORDT Art. Respiration im Handwörterbuch d. Physiologie; and SIBSON, Medico-Chirurgical Trans., vol. 31: also, QUAIN'S Anatomy, vol. I., p. 311. As to the gaseous interchanges, consult LAVOISIER, Expériences sur la Respiration, 1777; SPALLANZANI, Mémoire sur la Respiration, 1803; VIERORDT, Physiologie des Athmens, 1845; REGNAULT et REISET, Recherches chemiques sur la Respiration des Animaux des diverses classes, 1849; PETTENKOFER, Ueber den Respirations und Perspirations-apparat im physiologischen Institut zu München, 1860; and ANGUS SMITH, Air and Rain. Consult also article by BURDON-SANDERSON on Respiration in Handbook for Physiological Laboratory, p. 288; and articles by LAUDER BRUNTON, in British Medical Journal, 1875. An excellent account of the principles of ventilation is given in PARKE'S Hygiene.

V.—ASSIMILATION OR NUTRITION.

Having studied the history of the formation of blood, the mechanism by which it is circulated through the body, and the arrangements by which it receives new supplies of oxygen, and at the same time has carbonic acid removed, we have next to direct our attention to those intimate exchanges which are constantly taking place between the blood and the tissues. As has been already seen, every tissue is brought into close relation with the circulating blood by capillary arrangements. Any portion of living tissue may be regarded as being surrounded on all sides by minute capillaries in which a nutritious fluid is slowly passing along. In proportion to the activity of the tissue, the capillary plexus is more or less close and intricate. Thus, such tissues as the grey matter of the brain or voluntary muscle are supplied with so rich a plexus of capillaries as to bring each portion of the tissue into almost immediate contact with the circulating blood. On the other hand, in such tissues as cartilage, where vital phenomena occur with comparative slowness, the ultimate elements of the tissues exist at a considerable distance from the blood, and they are nourished by the transudation of fluids. In all tissues, however, matters are being constantly absorbed from the blood by the living protoplasmic elements. These matters may, under the influence of the tissue, either be converted into matter of the same nature as the tissue itself, be elaborated into more complex, or be split up into simpler, substances. For example, when a muscle works, chemical changes occur in it which lead to a destruction or degradation of at least some of the constituents of the muscle—the result being the formation of simpler chemical compounds. In this condition, the muscle is in a state of fatigue, which is recovered from when new materials are absorbed from the blood, and are used up in the renovation of the muscle-substance. Here, apparently, matters taken from the blood are converted into the substance of muscle. On the other hand, the protoplasm of a fat cell absorbs certain materials from the blood, which it elaborates into fat, either directly or indirectly, by first changing them into protoplasm and then into fat. In considering therefore the function of nutrition, it is convenient to describe (1) the interstitial phenomena, which include the passage of fluid matters from the blood to the tissues and the reabsorption of fluid by the bloodvessels; and (2) the ultimate changes which occur in the tissues themselves. Further, the phenomena of nutrition are closely connected with the formation and history of a substance, named *glycogen*, produced by the liver.

A.—INTERSTITIAL PHENOMENA IN NUTRITION.

It has been well remarked by Claude Bernard, that the blood may be regarded as an *internal medium*, in relation to which all the phenomena of nutrition take place. It is in a state of perpetual change, receiving on the one hand new materials from the outer world, or from the tissues; and on the other, giving up, in addition to the matters returned to the outer world by the various excretory channels, substances required for the nutrition of the tissues. It receives new materials, as stated on page 289, by various channels of absorption, and it gives up other matters by processes of elimination occurring in the lungs, skin, liver, kidneys, and bowels; and, as already mentioned, it supplies new materials to the tissues. Considered in relation to the tissues, two processes take place, namely, transudation and re-absorption.

1. Transudation of Nutritive Matter.

During its passage through the tissues, the blood gives up certain substances, namely, oxygen and other matters required for their repair. Each tissue appears to select from these substances such as are required for its existence; but it need scarcely be said that this expression does not imply the existence of any special power in the tissues, but simply that in accordance with physical and chemical laws, when any tissue is brought into relation with nutritive matters, these combine with the tissue. This power has been termed the *selective affinity of the tissues.* The process by which nutritive matters pass from the blood to the tissues is in all probability purely physical, governed by the laws which regulate the passage of matters from a moving fluid through an organic membrane. In the ultimate capillaries, such matters pass through a thin organic wall, formed of endothelial cells, and the change may be almost instantaneous. The rapidity of such diffusion will no doubt partly depend on the pressure of the blood in the capillaries, partly on the resistance offered by the tissues themselves, and partly on the pressure in the lymphatic channels. As to the rationale of the selective influence of the tissues, we are in absolute ignorance. It is only known, for example, that a fat-cell takes up certain materials to form fat, but the nature of the processes is still hidden.

Much discussion has taken place as to the part played by oxygen in nutrition. Some have supposed that it traverses the walls of the capillaries, so as to come into intimate contact with the tissues; whilst others have stated that the chemical phenomena resulting from the union of oxygen with certain constituents, do not occur in the tissues, but in the blood itself. It is probable that changes occur in both situations, but chiefly in the former. Blood in passing through the tissues undoubtedly loses its oxygen, and it has been shown that the introduction into the blood of any substance which consumes oxygen, such as yeast, interferes at once with the phenomena of nutrition. As has been already explained (p. 296), oxygen is carried to the tissues combined with $\underline{\underline{H}}$ as $\underline{\underline{H}}O$, but the physical conditions of temperature and pressure which lead to the separation of the O from the $\underline{\underline{H}}$ are unknown.

2. RE-ABSORPTION OF WASTE MATTERS.

The tissues give up to the blood CO_2 and waste matters. The proof of this statement is, that the blood returned from an active tissue contains an excess of these materials; but it is impossible to say whether the matters thus met with in the blood represent all the products of the tissue-changes, inasmuch as there is another fluid, the lymph, conveyed from the tissues, in which some of the waste products might be found. For evident reasons, our knowledge of the intimate phenomena of re-absorption is still very obscure, but the fact that it does occur is undoubted. It is important for the student to remember that each particle of living tissue gives up to, and receives from, the blood certain materials, and that in particular each absorbs oxygen and eliminates CO_2. There is thus a true respiration of tissues, and each living element, from this point of view, behaves like a microscopic aquatic organism.

B.—ULTIMATE CHANGES IN NUTRITION.

The changes in the tissues, which have been called ultimate, may be grouped under the terms Assimilation and Disassimilation. By assimilation is understood those changes by which the living tissues convert dead matter into matter similar to themselves; and by disassimilation, we mean those changes by which living matter, of complex chemical constitution, is resolved into simpler forms, in consequence of the activity of the tissue.

1. Assimilation.

Assimilation is intended for the repair of waste of tissue, and for growth. It has already been pointed out that nutritive matters transude from the bloodvessels into the tissues. These matters may be divided into two classes: (1) those (termed *constituent principles*) which are so assimilated as to enter into the intimate composition of living tissue, such as albuminous bodies, mineral matter, &c.; and (2) those (*auxiliary principles*) which are found in the fluid bathing the living tissue, and which do not enter into the constitution of the tissue itself, such as glucose, fat, &c. It is important to observe clearly this distinction. For example, some of the materials carried to a muscle by the blood may never enter into the constitution of the muscle substance, but are subjected in the muscle to certain chemical changes which form an integral part of the function of the muscle. Thus, it is probable that part of the heat produced in a muscle results from chemical changes occurring in carbo-hydrates carried to the muscle by the blood.

In attempting to follow the stages of the transformation of dead matter in the blood into the living matter, say of muscle, it may be observed that three stages occur: (1) *Fixation*, by which the albumen of blood passes into the state of albumen in the tissue-fluids; (2) *Transformation*, by which the albumen of the tissue-fluids is converted into the myosine of muscle; and (3) *Vivication*, by which the myosine thus formed passes into the living state, and manifests the phenomena of irritability, contractility, &c. There is no doubt this is a very artificial mode of describing the changes, the various steps of which are at present only matter of conjecture, but it assists the mind in understanding the nature of the processes.

The formation of the anatomical elements of the tissues is intimately related to their histological structure. Without entering into details, it may be pointed out here that all the tissues are built up of water, mineral matters, albuminous bodies, fats, and carbohydrates. The importance of the first two has been already alluded to at pp. 26, 211-213, and it is only necessary here to consider the formation of albumen, fats, and carbohydrates.

a. *Origin of Albuminous Matters.*

All albuminates are derived from nitrogenous foods. It has already been seen that the various albuminous articles of food are converted by digestive processes into peptones, and it has been assumed that in one way or another these peptones are converted into the albumen of the blood. This is the generally received theory. But, if solutions of peptones be introduced directly into the blood, there is an increase of the nitrogenous matters separated by the kidneys, even whilst there were no conditions, such as severe muscular exercise, favouring waste of tissue. Consequently, Fick and others have supposed that the peptones are never actually incorporated with tissue, but only undergo changes subject to its influence; and that the albuminous constituents of the tissues must be derived from albumen directly absorbed.

b. *Origin of Fats.*

The principal portion of the fats stored up in the body is derived from the fatty matters introduced in the food, but the exact stages through which the matter passes from the state of fat as it exists in the food to the semi-fluid condition in a living fat-cell are unknown. In Carnivora, undoubtedly, the greater portion of the fat is thus obtained; but in Herbivora, and in many other animals, its appearance cannot thus be accounted for. Thus, bees form wax, a kind of fat, from saccharine substances obtained from flowers; and geese fed on grain, which contains only a small amount of fat, store up large quantities of this substance. Dumas states that the Indian corn or maize on which a goose is fed contains 9 per cent. of fat, and on calculating the quantity consumed, he found more fat in it than was sufficient to explain the increased weight of the goose. These conclusions were confirmed by the careful and extensive observations of Boussingault. Liebig, however, made several very ingenious experiments upon swine. He says that three pigs, to be fattened in thirteen weeks, require 1,000 lbs. of pease and 6,825 lbs. of boiled potatoes. These contain together 26 lbs. of fat—21 lbs. in the pease, and 5 lbs. in the potatoes. One fattened pig gives on an average 50 to 55 lbs. of fat—that is, the three together, 150 to 165 lbs. Each animal, before being fattened, contains, on an average, 18 lbs. of fat—that is, 54 lbs. for the three. If to these 54 lbs. we add 26 lbs. from the food, we get 80 lbs.; and if we subtract these from 150 lbs. to 165 lbs., there is a remainder of 70 to 85 lbs. of fat produced from the starch, &c., contained in the food. These experiments have been confirmed by the more recent researches of Messrs. Lawes and Gilbert, who found that, in fattening pigs, for every 100 parts of fat in the food, the animals stored up from 400 to 450 parts of fat in their bodies. (*Hughes Bennett.*)

It is evident, therefore, that fats may be formed from other substances than the fat introduced in the food. Liebig suggested the theory that they were derived from carbohydrates. He supposed that one part of the carbohydrates introduced in the food was oxidised into water and carbonic acid, whilst the remainder was transformed into fat. The objections to this theory are that chemists have found it impossible to transform carbohydrates into fats, and that when animals are fed on carbohydrates alone, the amount of fat formed decreases. Voit has suggested that the carbohydrates do not contribute directly to the formation of fat, but indirectly, by assisting in the decomposition of albuminates.

It is now generally accepted by physiologists that a considerable part of the fat of the body is formed from albuminates. This view is supported by various well-known facts. Thus, when albuminous tissues in the dead body are subjected to the action of water, a fatty substance called *Adipocire* is frequently formed. Animals have also become fattened on a diet of pure caseine. Pettenkofer and Voit have shown that after a flesh diet, all the nitrogen appears in the excretions, whilst a proportion of the carbon is retained in the organism; entering, probably, into the formation of fat. Further, as shown by Pavy, any albuminous substance may be supposed capable of being decomposed into a nitrogenous portion of simpler constitution, and into a non-nitrogenous residue, which may become transformed into fat. It is impossible, however, to say whether the albuminous matter thus decomposed has already existed in the tissue or has been derived from the blood.

There are thus evidently two sources of fat: (1) the fat contained in the food, and (2) from transformations in the albuminous matters of food. The part played by the carbohydrates is in all probability to combine with a certain quantity of oxygen, forming carbonic acid and water, thus preventing oxidation of the non-nitrogenous residue already alluded to as proceeding from decomposition of albuminates. It is well known that circumstances hindering decomposition of albuminates and oxidization processes, such as deficient muscular exercise and deficient respiration, favour the formation of fat.

When the amount of fat in the body passes a certain limit, the condition is termed *obesity*. To remove this state it is necessary to attend to the following points: (1) no fat to be taken in the food; (2) active muscular exercise to be indulged in for the purpose of increasing oxidation processes; and (3) no carbohydrates, but only albuminates, in the form of lean meat, to be taken, so as to allow the oxygen introduced in respiration to attack the non-nitrogenous residue produced by the decomposition of the albuminates, and thus prevent the formation of fat. These are the scientific principles lying at the base of the well-known empirical system of Banting, which is often followed with remarkable success.

2. DISASSIMILATION.

This process is always carried on in the presence of oxygen, and we would therefore assume that one of the first steps is the liberation of O from $\underline{\underline{\mathrm{H}}}\mathrm{O}$. The O thus liberated enters into combination with certain of the elements of the tissues, so as to produce numerous chemical compounds; and as the result of this union, energy is set free under various forms, such as heat, movement, &c. Again the difficulty presents itself of being able to ascertain how much of the O enters into combination with the elements of the tissue, and how much with the auxiliary constituents. Suppose, for example, the mechanical work of a muscle to be represented by 10; of this, 2 may be produced by oxidation of muscle substance and 8 by that of auxilliary matters; but suppose the work of the muscle to be 30, and that only 18 are represented by the auxiliary substances, it is evident that the remaining 12 must have been contributed by changes in the muscle substance. The practical fact however, remains, that activity of tissue is associated with the production of simpler chemical compounds than existed in the tissue itself. It is beyond the limits of this work to describe in detail the disassimilation processes which have been followed by physiological chemists, but a few may be given here by way of illustration.

a. *Disassimilation of Nitrogenous Matters.*

1. *Pigments.*—The pigments of the *bile*, bilirubine, $C_{16}H_{18}N_2O_3$, and biliverdine, $C_{16}H_{20}N_2O_5$, are derived from the decomposition of the colouring matter of the blood, hæmoglobine. One of the pigments of the *urine*, urobiline, $C_{32}H_{40}N_4O_7$, is derived from bilirubine, a transformation which probably occurs in the intestinal canal. The other pigment of the urine, indican, or uroxanthine, $C_{26}H_{31}NO_{17}$, is believed to be formed by the union of indol, C_8H_7N, one of the products of the decomposition of albuminous substances by the action of the pancreatic juice, with some substance containing oxygen. This statement is founded chiefly on the fact that the subcutaneous injection of indol is followed by the appearance in the urine of a large quantity of indican.

2. *Bile Acids.*—These are probably formed by the union of a non-nitrogenous acid, cholalic, $C_{24}H_{40}O_5$, with two nitrogenous bases, glycocolle, $C_2H_5NO_2$, and taurine, $C_2H_7NSO_5$.

3. *Urea.*—It is well known that this substance, CH_4N_2O, is derived from albuminous matters, through a series of intermediate decompositions, the steps of which have not yet been accurately traced. There can be no doubt that one of the first compounds formed by the decomposition of albuminous bodies is uric acid, $C_5H_4N_4O_3$, and that urea may be produced by the oxidation of this substance. If uric acid be introduced into the circulation, there is an

increase of urea excreted in the urine, and frequently also at the same time an increased quantity of oxalate of lime. Animals living upon a highly nitrogenous diet, and in which the respiratory processes occur slowly, usually excrete a large quantity of uric acid. Such is the case in serpents; but as it is well known that the fæces of birds, whose respiratory activity is very great, also contain a large quantity of uric acid, there are grounds for supposing that, in some circumstances, the origins of urea and uric acid are different. Various opinions are held as to where urea is formed. Some have supposed that it originates from the decomposition of coloured blood corpuscles in the liver, inasmuch as it is always found in this organ, and as it diminishes or may even disappear from the urine in acute atrophy of the liver. Others have held that it may be formed in other organs, such as the lungs, spleen, brain, &c.; whilst some have suggested that it is produced in great part in the kidneys themselves. The latter view seems to be untenable. The blood of the renal artery contains more urea than the blood of the renal vein, and when the kidneys do not efficiently perform their functions, or are extirpated, urea accumulates in the blood.

4. *Uric Acid.*—This acid, $C_5H_4N_4O_3$, is related to the following nitrogenous compounds: Guanine, $C_5H_5N_5O$; sarcine, $C_5H_4N_4O$; and xanthine, $C_5H_4N_4O_2$, and it has been obtained by chemical means from one or other of these bodies. All of these substances have also been met with in glands, such as the liver and pancreas, the spleen, the thymus, and in muscles. Meissner has supposed that in reptiles and birds, it originates principally in the liver, whilst others have thought that it might be partly derived from the decomposition of colourless blood corpuscles, or of connective tissues. The latter views are based upon the pathological facts of the increased formation of uric acid in

leucocythæmia and in the gouty diathesis. The important practical fact to remember is, that it is produced from nitrogenous substances. Closely related to it is the substance known as allantoine, $C_4H_6N_4O_3$, met with in the urine during fœtal life and after birth during lactation. The following formulæ represent various possible reactions resulting from the decomposition of uric acid, and which may account for the appearance in the urine of some of the substances mentioned.

$$\underset{\text{Uric acid.}}{C_5H_4N_4O_3} + H_2O + O = \underset{\text{Alloxan.}}{C_4H_2N_2O_4} + \underset{\text{Urea.}}{CH_4N_2O}$$

$$\underset{\text{Alloxan.}}{C_4H_2N_2O_4} + O = \underset{\text{Parabanic acid.}}{C_3H_2N_2O_3} + CO_2$$

$$\underset{\text{Parabanic acid.}}{C_3H_2N_2O_3} + H_2O = \underset{\text{Oxaluric acid.}}{C_3H_4N_2O_4}$$

$$\underset{\text{Oxaluric acid.}}{C_3H_4N_2O_4} + H_2O = \underset{\text{Urea.}}{CH_4N_2O} + \underset{\text{Oxalic acid.}}{C_2H_2O_4}$$

$$\underset{\text{Allantoine.}}{C_4H_6N_4O_3} + 5H_2O = \underset{\text{Oxalic acid.}}{2C_2H_2O_4} + 4NH_3$$

5. *Various Nitrogen Bases.* — These are — Creatine, $C_4H_9N_3O_2$; creatinine, $C_4H_7N_3O$; guanine, $C_5H_5N_5O$; sarcine, $C_5H_4N_4O$; and xanthine, $C_5H_4N_4O_2$. All have been found in muscle-serum, and are believed to originate from the transformation of albuminous matters. In all probability they are steps in the formation of uric acid.

6. *Leucine*, $C_6H_{13}NO_2$, and *tyrosine*, $C_9H_{11}NO_3$, are derived from albuminous matters by the action of the pancreatic juice. Leucine has been found in many glands.

7. *Cystine*, $C_3H_7NSO_2$, is a substance found in bile, and is formed from albuminous matters. It is nearly related to *taurine*, $C_2H_7NSO_3$, one of the constituents of the bile acids, but it has not been demonstrated that the one may be transformed into the other.

8. *Lecithine*, $C_{44}H_{90}NPO_9$; *neurine*, $C_5H_{15}NO_2$; and *phos-*

phoglyceric acid, $C_3H_9PO_6$, are products obtained by the decomposition of nervous matters, but the steps leading to their formation are practically unknown.

b. *Disassimilation of Non-nitrogenous Matters.*

All non-nitrogenous substances are finally resolved into carbonic acid and water; but, in the course of transformation, various intermediate bodies may be formed. Thus, the various volatile fatty acids, formic, acetic, propionic, butyric, &c., may result from the decomposition of fats, whilst lactic acid may be formed from carbohydrates. The following formulæ show how glucose may be ultimately resolved into carbonic acid and water, and it will be observed that at each step, with the exception of the first, CO_2 and H_2O are formed:—

$$\underset{\text{Glucose.}}{C_6H_{12}O_6} = \underset{\text{Lactic acid}}{2C_3H_6O_3}$$

$$\underset{\text{Lactic acid.}}{2(C_3H_6O_3)} + 2O = \underset{\text{Butyric acid.}}{C_4H_8O_2} + CO_2 + 2H_2O$$

$$\underset{\text{Butyric acid.}}{C_4H_8O_2} + 3O = \underset{\text{Propionic acid.}}{C_3H_6O_2} + CO_2 + H_2O$$

$$\underset{\text{Propionic acid.}}{C_3H_6O_2} + 3O = \underset{\text{Acetic acid.}}{C_2H_4O_2} + CO_2 + H_2O$$

$$\underset{\text{Acetic acid.}}{C_2H_4O_2} + 3O = \underset{\text{Formic acid.}}{CH_2O_2} + CO_2 + H_2O$$

$$\underset{\text{Formic acid.}}{CH_2O_2} + O = \underset{\text{Carbonic.}}{CO_2} + \underset{\text{Water.}}{H_2O}$$

Lactic acid, $C_3H_6O_3$, is chiefly produced in the muscles by the decomposition of glucose formed from glycogen, a substance produced in the liver. Oxalic acid, $C_2H_2O_4$, may be derived either from nitrogenous or from non-nitrogenous substances. Thus:—

$$\underset{\text{Creatine.}}{C_4H_9N_3O_2} + 2O = \underset{\text{Oxalic acid.}}{C_2H_2O_4} + \underset{\text{Methylamine.}}{C_2H_7N_3}$$

$$\underset{\text{Glucose.}}{C_6H_{12}O_6} + 5O = \underset{\text{Oxalic acid.}}{2(C_2H_2O_4)} + 2CO_2 + 5H_2O$$

In normal circumstances, the amount of oxalic acid formed is very small, but in a state known as the *oxalic acid diathesis* or *oxaluria*, it may be formed in considerable quantity. When so produced, it appears in the urine as oxalate of lime.

Cholestrine, $C_{26}H_{44}O$, is a substance richer in carbon than any other non-nitrogenous substance. Flint has stated that it is produced chiefly from nervous matter, and he supposes further that it is eliminated from the blood by the liver. Now it is well known that this substance may be readily extracted from brain-matter by strong alcohol, and that it exists in bile and forms the chief part of gall-stones, but it is not easy to trace the connection between the two facts. It exists in the yolk of egg, and in fœtal tissues, where there are no nervous elements, observations which show that it cannot be regarded simply as one of the products of the decomposition of nervous substances.

The two ultimate products of the disassimilation of non-nitrogenous matters are carbonic acid and water. With regard to the first, it may be observed that it is partly obtained from the oxidation of carbohydrates, fats, and vegetable acids, and partly from albuminous substances. It has been estimated that about one-fifth part of the CO_2 eliminated is derived from albuminates. The amount of water actually formed in the body is very small, and it is produced by the excess of oxygen introduced in inspiration over what is returned in expiration.

c. *Disassimilation of Mineral Matters.*

Many organic acids, such as malates, tartrates, &c., are converted into carbonates. Thus, the urine of herbivora contains more carbonates than that of carnivora. The phosphates are derived exclusively from food, except a very small amount which may be produced by the decomposition of lecithin or phospho-glyceric acid. A part of the sulphates arises from the sulphur of the albuminous compounds, and it is probable, as suggested by Salkowsky, that cystine and taurine are intermediate products in this disassimilation. He also showed that all the sulphur of the albuminous bodies is not eliminated as sulphates.

C.—THE PRODUCTION OF SUGAR OR GLYCOGENY.

The phenomena of nutrition are intimately related with the formation by the liver of a substance called *glycogen*, and with the changes which it undergoes in the tissues. This remarkable function of the liver was first pointed out, in 1849, by Claude Bernard. Since that date, numerous researches have been made by Bernard, Pavy, MacDonnell, and others, which have not only modified several of the views first enunciated by Bernard, but have thrown much light on the exact nature of the process, the ultimate destination of glycogen, and the relation of the function to the nervous system.

1. Nature of Glycogen.

If the liver be quickly removed from the body of a well nourished animal during digestion, cut in pieces, and thrown into boiling water, the morsels become in a few minutes firm and crisp, and an opalescent or yellowish brown solution is obtained. Add to this fluid about two-thirds of its volume of 40 per cent. alcohol, and a flocculent white precipitate will fall, which may be collected on a filter and dried. This precipitate is impure glycogen. To obtain it quite pure, it must be boiled for a quarter of an hour in a strong solution of potash; neutralize the carbonate of potash with acetic acid, and reprecipitate the glycogen with alcohol. When so obtained, it is an amorphous, colourless, inodorous powder, soluble in water, and insoluble in alcohol and ether. Boiling hydrochloric acid converts it into dextrine. It gives a violet colour with iodine, reduces hydrated oxide of copper, and rotates to the right a polarized ray of light. It is represented by the formula $C_6H_{10}O_5$, and is in all respects similar to starch.

The amount of glycogen in the liver has been found to vary in different species of animals. Thus, according to MacDonnell:

	Ratio of weight of body to weight of liver.	Percentage of Glycogen.
Dog,	30·1	4·5
Cat,	19·1	1·5
Rabbit,	35·1	3·7
Guinea-pig,	21·1	1·4
Rat,	26·1	2·5
Pigeon,	44·1	2·5

Glycogen has also been found in the liver of invertebrate animals. It exists in greatest amount two or three hours after a full meal; and it is diminished by fasting. After death, it quickly disappears, being converted into glucose.

2. ORIGIN OF GLYCOGEN.

The amount of glycogen formed is largely influenced by the nature of the food. Carbohydrates are converted by the digestive fluids into glucose, and the glucose passes into the portal system. In the hepatic cells, a simple dehydration may occur, with the result of forming glycogen. Thus:

$$\underset{\text{Glucose.}}{C_6H_{12}O_6} - H_2O = \underset{\text{Glycogen.}}{C_6H_{10}O_5}$$

Bernard has found that the injection of sugar into the portal vein is followed by an increased formation of glycogen.

But the substance may be produced even after the careful exclusion of all carbohydrates from the food. It has been supposed by some that it may be partly derived from fats. Thus, the injection of olive oil or of glycerine into the alimentary canal has been said to have caused an increase; but the experimental evidence is doubtful. As regards the possible origin of glycogen from albuminous matters, great doubt exists. An excess of gelatine in the food usually causes increased production. The injection of albumen into the stomach is followed by no increase; but Bernard, Kühne, and most physiologists are inclined to hold that in the liver albuminous matters split up into a nitrogenous portion,—possibly urea—and a non-nitrogenous portion, which may become glycogen. But it is remarkable that glycogen may be formed even during complete starvation, and that it accumulates in the livers of hybernating animals, whilst these are taking no nourishment. It would thus appear that, under some circumstances, glycogen may be formed independently of matters furnished from the alimentary canal. The presence of glycocine in one of the bile acids (glycocholic) has suggested to Kühne and Heynsius the notion that it may split up into urea and glucose, the latter being afterwards converted into glycogen; and they have found that the introduction of glycocine directly into the blood is followed by an increase in the amount of urea in the liver and urine, and of glycogen in the liver.

3. SUGAR OF THE LIVER.

If a few morsels of liver, an hour or two after the death of the animal, be thrown into boiling water, so as to make an infusion, and the infusion be tested for sugar, it will be found that a large amount of this substance is present. A still more satisfactory demonstration may be obtained by introducing the nozzle of a syringe into the portal vein, so as to wash out the liver with cold water—the washings being collected at intervals from the hepatic vein. On testing the washings, it will be found that the first portions contain a large amount of sugar, and that the amount diminishes in each successive portion, until no reaction is obtained. If, however, the operation be repeated two hours afterwards, the presence of sugar will be again indicated. As a rule, a perfectly fresh liver, that is, one removed quickly from an animal just killed, and thrown into boiling water, shows only faint traces of sugar; but if it be left for even a few minutes to a temperature of 60° Fah., sugar is present in abundance. Immediately after death, there is apparently a rapid transformation of glycogen into sugar. Thus, Dalton found 1·8 of sugar per 1,000 after five seconds, 6·8 after fifteen minutes, and 10·3 after an hour. Pavy has strongly held that the formation of sugar is a post-mortem phenomenon, and that it never exists during life; a view which has been contested chiefly by Claude Bernard. The latter physiologist has shown that even in the living animal, whilst the blood of the portal vein gives no trace of sugar, the blood of the hepatic vein always contains a small quantity. The fact appears to be that even during life a very minute quantity may be present, and that the amount increases rapidly after death. The author, in class demonstrations, has always found it impossible to prove to students the entire absence of sugar from a perfectly fresh liver.

4. TRANSFORMATION OF GLYCOGEN INTO SUGAR.

In 1855, Claude Bernard showed that glycogen is transformed in the liver into glucose under the influence of a ferment which exists in the liver itself. He also pointed out that the transformation is at once arrested by plunging the liver into water at 100°C. or into water at 0°C.; and he explained these facts by stating that the extremes of heat and cold coagulated, or otherwise changed, the fermentive matter. The isolation of this ferment presented great difficulties, but Bernard has succeeded in extracting it from the liver by means of glycerine. It is interesting also to find that he has proved the identity as regards chemical activity between the ferment thus separated from the liver and the diastase of germinating grain. Thus, Claude Bernard has discovered another point of resemblance between animal and vegetable organisms. He was the first to show that a substance precisely similar to starch was formed in the animal body; and he has now completed his labours by demonstrating the existence in the animal body of a fermentive matter similar to what converts the starch of the germinating grain into sugar.[1]

5. SUGAR IN THE BLOOD.

The presence of sugar in the blood of diabetic patients has been long known, but its relation to the glycogenic function of the liver was first pointed out by Claude Bernard. If a dog be fed with flesh free from sugar, whilst the blood of the portal vein will contain none, some will be found in that of the hepatic vein, the inferior vena cava, the right heart, and the arterial system generally. In this case, therefore, the sugar does not disappear in the lungs, but in the capillary system. On the other hand, if the diet supply a considerable quantity of glucose, it is absorbed, and is

---

[1] The author has frequently obtained glycerine-extracts of liver which convert starch into sugar. He has also ascertained that glycerine-extracts of other organs, such as lung, brain, spleen, and muscle, have sometimes the same effect, though to a feebler degree. The extract of muscle rarely fails. This observation indicates that the ferment may exist in other organs than the liver.

found in variable amount in the vena porta. Sometimes even the amount in the vena porta is greater than in the hepatic vein, but the amount in the general system of vessels is not proportionately increased. Thus it would appear that the amount of sugar in the portal vein depends on the nature of food, whilst the amount in the hepatic veins and general system depends on the activity of the liver. Bernard has found ·9 per 1,000 in the blood of man, 1·7 in the ox, ·99 in the calf, and ·91 in the horse.[1] When the amount is largely increased, it is separated by the kidneys, and the state is known as glycosuria or diabetes.

6. Transformation of the Sugar in the Blood.

It was at one time supposed that the sugar entirely disappeared by oxidation in the lungs, a view which was apparently supported by the anatomical arrangements, and by the fact that glucose is very oxidizable, more especially in an alkaline fluid, such as the blood. But it is negatived by the fact that the quantity of sugar in the blood of the left heart is not much less than that in the right heart, and that sugar is also found more or less in the blood of all

---

[1] Pavy has recently, in communications to the Royal Society, disputed the accuracy of Bernard's methods of analysis, and has given an elaborate account of his own. He has been unable to support Bernard's statement that there is less sugar in the blood of the venous than in that of the arterial system, and therefore he objects to the theory urged by Bernard, that sugar disappears in the capillaries. He also shows that the sugar in blood gradually disappears after death, the blood becoming acid from the development of lactic acid. So far as the author can judge, Bernard has brought forward sufficient evidence to show the probability of his theory being correct, but the demonstration does not amount to proof. While disputed by so able and accurate an observer as Pavy, the matter must still be regarded as *sub judice*, and demanding fresh investigation.

tissues, and especially in muscles. Physiologists generally are now of opinion that the sugar is used up chiefly in the muscles, and that in some way it contributes to their activity and the production of heat. It has been ascertained that after a muscle has been tetanized, it contains less sugar than before, and the appearance of diabetes during the action of curare, a substance which completely paralyzes all voluntary muscles, has been accounted for by supposing that the inactive muscles do not consume the glucose supplied to them, and that consequently this substance accumulates in such quantity in the blood as to be eliminated by the kidneys. As regards the rôle of glucose in supporting animal heat, no satisfactory evidence has as yet been afforded, the only experimental fact being the alleged fall of temperature in animals from whom, by a strict diet, all external supplies of glucose have been cut off. Finally, it is not at all improbable that a portion of the glycogen or glucose may contribute to the upbuilding or histogenesis of tissues, a statement which is supported by the well-known fact that these substances abound in embryonic tissue, where histogenetic changes occur with great rapidity.

7. Relation of the Nervous System to Glycogenesis.

Claude Bernard was the first to point out that a puncture of the floor of the fourth ventricle, at the origin of the pneumogastric nerves, produced temporary diabetes, that is, the appearance of sugar in the urine. The seat of the puncture is shown in Fig. 115.

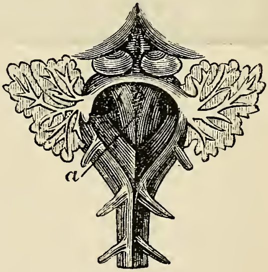


Fig. 115.—Posterior view of the Medulla Oblongata, and part of the Cerebellum of a rabbit. *a*, situation of the puncture followed by diabetes.

After the operation, the vessels of the liver are dilated and engorged with blood. There appears to be a vaso-motor paralysis in the liver. Diabetes has also been observed to follow injury of the cerebral lobes in man, of the cerebellum, of the cerebral peduncles, pons Varolii, middle peduncle of the cerebellum, and of the cervical sympathetic cord and sciatic nerve. Cyon and Aladoff have endeavoured to trace the nervous communications by which these effects may be produced, and the results of their researches, as applied to man, are given in Fig. 116.

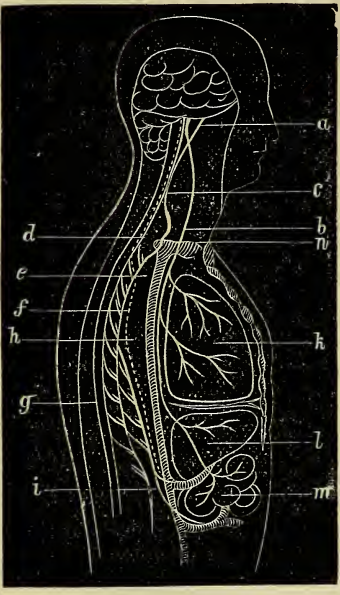


Fig. 116.—Diagram showing the course of the vaso-motor nerves of the liver, according to Cyon and Aladoff. These nerves are indicated by the dotted line which accompanies them: *a*, vaso-motor centre; *b*, trunk of the vagus; *c*, passage of the hepatic vaso-motor nerves from the cord along the vertebral artery; *d*, fibres going on each side of the subclavian artery, and forming the annulus of Vieussens; *e*, first dorsal ganglion; *f*, gangliated cord of the sympathetic; *g*, the spinal cord; *h*, splanchnic nerves; *i*, cœliac ganglion, from which vaso-motor fibres pass to the hepatic and intestinal vessels; *k*, the lungs, to which the fibres of the vagus are seen to be distributed; *l*, the liver; *m*, intestine; and *n*, the arch of the aorta. (*Lauder Brunton.*)

As has already been seen in studying the innervation of bloodvessels, p. 367, the vaso-motor centre from which constant stimuli pass to all the vessels of the body, so as to keep these in a state of moderate contraction, is situated in the medulla oblongata. The vaso-motor fibres for the liver pass from the centre down the spinal cord for a certain distance, and issue from thence into the sympathetic, and by it through the splanchnics to the liver. Cyon and Aladoff state that they leave the cord by fibres, *c*, which accompany the vertebral artery, passing in them to the lower cervical ganglion. From thence they proceed in two bundles, *d*, one of which passes on either side of the subclavian artery, forming the annulus of Vieussens, to the first dorsal ganglion, *e*, and thence through the gangliated cord of the sympathetic, *f*, to the cœliac ganglion, *i*, and along the hepatic vessels to the liver. (*Lauder Brunton.*) If these nerves be divided at any point, it is evident that vaso-motor paralysis will occur in the liver, the vessels dilate, the flow of blood through the liver is increased, and there may be an increased production of sugar. It appears that section of the sympathetic cord between the tenth and twelfth ribs, and section of the splanchnics, may be performed without sugar appearing in the urine, a somewhat perplexing fact which has been explained by Cyon as follows: He points out that "it is not mere dilatation of the hepatic vessels, but increased circulation through them, which accelerates the formation of sugar; and the width of the vessels is of little consequence unless there be sufficient blood to fill them. Now, the vessels of the intestine, especially when the digestive canal is long, as it is in rabbits, are so capacious that, when dilated, they can hold as much blood as all the rest of the vascular system put together, and their vaso-motor nerves are also contained in the lower part of the cord and in the splanchnics. Consequently, when these are divided, the vaso-motor nerves of the intestine become paralysed as well as the hepatic ones, the vessels themselves dilate, and retain so much blood that there is not left enough to increase the flow of blood through the liver, even though its vessels may be standing wide open to receive it. But if the vessels of the liver be first dilated, and the cord and splanchnics be then cut, the formation of sugar is not arrested; for the liver, having once a brisk circulation established in it, keeps it up, although the intestinal vessels may have become dilated." (Lauder Brunton's Lecture, Brit. Med. Jour., 1874, p. 40.) It is evident also that the hepatic vessels may become dilated not only by direct interference with the vaso-motor centre, but by an inhibitory effect on this centre exercised by sensory nerves. Thus if the pneumogastric be cut in the neck, stimulation of the lower end produces no effect on the liver; but if the upper end be irritated, the vessels of the liver dilate, the circulation increases, and sugar appears in the urine. This is to be explained by certain fibres of the pneumogastric exercising an inhibitory influence over the vaso-motor centre. The hepatic vessels may also be reflexly dilated by irritation applied to the vagus, either at its ends in the lungs, liver, or intestine, in its trunk or at its roots in the medulla, or to the cerebrum, cerebellum, pons, and probably some of the sympathetic ganglia. (*Lauder Brunton.*) Any marked increase in blood pressure affecting the vessels of the liver may cause increased production of sugar, and its appearance in the urine. Interference with the vaso-motor centre or nerves will chiefly affect the calibre of the hepatic artery, which becomes dilated. As this is followed by increased production of sugar, the inference is that the blood of the hepatic artery may carry to the liver the materials for forming the glycogenic ferment.

Consult regarding the glycogenic function of the liver, LAUDER BRUNTON'S admirable lectures in the British Medical Journal, 1874, where numerous references to original papers are given, and our knowledge of the physiology of the production and consumption of sugar is applied to the explanation of many of the phenomena of diabetes. The latest communications on this subject by two distinguished observers, who have devoted special attention to the subject, are: CLAUDE BERNARD, Critique Expérimentale sur le Mécanisme de la Formation du Sucre dans le Foie, Annales de Chimie et de Physique, Novembre, 1877; and F. W. PAVY on the Physiology of Sugar in relation to the Blood, communicated to the Royal Society in July, 1877.

CONDITIONS OF HEALTHY NUTRITION.

The conditions of healthy nutrition are as follows:—

1. *A proper supply of blood.*—If the principal vessel of a limb be ligatured, the limb becomes for a time cold and powerless until the circulation be re-established through collateral vessels; but if the supply of blood be entirely cut off suddenly, as by ligaturing all the vessels, moist gangrene soon appears; if more slowly and gradually, as by pathological changes in the vessels, dry gangrene is the result, as may be seen in the senile gangrene of aged people, or in the form caused by the action of ergot of rye. On the other hand, actively growing parts have always a rich supply of blood.

2. *A proper quality of blood.*—As already explained on p. 205, this implies that all the processes of nutrition are properly performed. If one of these processes be disturbed, the nutrition of the body as a whole, or of an organ of the body, is affected. By the due performance of all of these processes, the blood is maintained in a healthy state. It is remarkable that in a vigorous individual, if the blood become vitiated, there appears to be an effort on the part of the various excretory organs to get rid of the noxious matter. Thus, during the course of fevers, and more especially in what physicians have long recognized as the *critical stage*, or *crisis*, there may be diarrhœa, profuse diaphoresis or sweating, epistaxis, or bleeding at the nose, or the appearance of large quantities of urates in the urine, after which the individual may proceed towards recovery. Sir James Paget has pointed out many interesting examples of how the nutritive changes occurring in one organ may affect the whole body. Thus the development of the beard in men, of the mammæ in women, and the changes in form more or

less of the whole body, are examples of nutritive changes associated with the appearance of the capacity for reproduction at the age of puberty, indicating that there is some kind of correlation between the nutrition of the reproductive organs and of other parts of the body. The same fact is illustrated by what is seen in the lower animals. Thus, in the majority, the two sexes are alike until the time of puberty, when a divergence occurs, as may be seen in the greater size of the male, and in the development of various epidermic appendages, such as the mane of the lion, the comb of the common cock, and the magnificent tail feathers of many birds. These facts have been included under the term *complemental nutrition*, the idea being that the nutrition of one part is the complement of the other, and is intimately associated with it.

It would appear also that all tissues are liable to the two following influences: (1) if the nutrition of a tissue be affected by some external influence, such as the action of the vaccine virus, or the poison of any of the eruptive fevers (small-pox, scarlatina, measles), the nature of the tissue is so profoundly altered as to give it an immunity from the action of the virus for a considerable time; and (2) that a tissue so altered tends slowly to revert to its original condition, just as a reversion to some ancestral form may be observed, as pointed out by Darwin, in artificial races of pigeons and dogs. These views, ably urged by Sir James Paget, afford a rational explanation of the influence exerted by vaccination over the body, an influence so profound as to secure the individual against an attack of unmodified small-pox for sixteen or seventeen years, beyond which time, however, the tissues slowly return to their original state.

Again, if we consider the phenomena of nutrition as consisting essentially in molecular change, it is necessary to assume as an explanation of the persistence of form for perhaps many years, that each living element of tissue so operates upon the nutritive matter brought to it by the blood as to convert it into matter almost precisely similar to itself. Thus, we may conceive particle by particle removed and the edifice still having the same form, inasmuch as fresh particles precisely similar are introduced. But it is significant that slow changes do occur. A tissue apparently is not kept in exactly the same condition for any length of time. During the early period of life, it advances to a condition of greater strength and higher vitality; but afterwards, when a maximum has been reached, it slowly retrogrades until the tissues of old age are unlike those of youth.

3. *A healthy state of the tissue itself.*—A healthy tissue will continue in this state unless a strong influence be exerted upon it. If it become what we term unhealthy, that is, if nutritive changes of a different kind or of a different intensity are induced, this morbid condition also tends to become perpetuated. Thus we may explain the persistence of tumours, either simple or what are called malignant, and the inveteracy of many diseases of the skin. But even in pathological conditions, the same law of a tendency of a reversion to what may be called the normal type may be observed.

4. *A certain influence of the nervous system.*—Section of a motor nerve is followed by wasting of the muscles supplied by it. Section of a nerve supplying the bloodvessels of an area of mucous membrane or of skin causes ulceration and destruction of the part. The limbs of the paralytic waste, unless the muscles be frequently artificially excited to contract. These facts show the influence of the spinal cord and motor portions of the nervous system; but it is not easy to account for the well-known influence of psychical conditions. There is scarcely an organ of the body the functions of which may not be more or less affected by various conditions of the

mind. Thus joy or sorrow, a light heart or a mind brooding with anxiety, exercise an influence over the nutrition of the body. As a rule, a contented and happy frame of mind and freedom from care favour nutrition; whilst worry or melancholy diminish it. Again, hope and confidence seem to be favourable towards recovery even from serious diseases, but fear and foreboding of evil may aggravate even simple maladies and tend to make dangerous ones fatal. When the exact physiological processes associated with psychical states are understood, these facts may be accounted for.

GROWTH.

Growth may be either special or general. Thus we may have growth of a particular organ, as in the development of the thymus gland during fœtal life, the increase in the size of the uterus during pregnancy, or the increase in the size of the muscles of the arm following severe but regular muscular exercise. When growth is limited, it may be termed *hypertrophy*, or increase of growth, as opposed to *atrophy*, or diminution. Again, growth may be general, affecting not one tissue or one organ, but the whole body, as occurs in early life. Regarding nutrition as consisting essentially in processes of assimilation and disassimilation, it will be seen that when the first is in excess there is growth; when both are equal, there is decline; and when the second is in excess, there is wasting.

From the histological point of view, growth may consist: (1) of an increase in the volume of tissues already existing; (2) of the development of the elements of other tissues which previously existed in an undeveloped state; and (3) of both of these changes. Thus, the walls of the uterus, in the virgin state, are thin and contain only a comparatively small number of involuntary fibres. During pregnancy, however, numerous fibres are probably produced from nucleated protoplasms hitherto in an undeveloped state, so that the wall of the organ becomes thick and powerful. The same phenomenon, though to a less degree, probably occurs in such a voluntary muscle as the biceps. With regular exercise, this muscle, in man, may become at least one-third thicker than what it would be if kept in a state of inactivity. But the size of the individual fibres is unaltered, and the increase in thickness appears to be due to the development of new fibres, the elements of which previously existed. It cannot be said that the last statement has been proved, and it may be that activity of a muscular fibre not only strengthens this individual fibre, but, by division or budding of protoplasmic elements, may lead to the production of new fibres.

The following conditions favour growth : (1) activity; (2) increased supply of blood; (3) integrity of the nervous system.

No satisfactory explanations have yet been given of the causes of arrest of growth. What are the conditions that determine the maximum size of an organ or of a muscle, or the bulk of an animal? Such enquiries are too speculative to fall within the plan of this work.

Consult PAGET'S Surgical Pathology, edited by TURNER, Lects. I.-III.; HERBERT SPENCER'S Principles of Biology, vol. I., p. 107.

VI.—SECRETION.

Whilst the blood is passing through the vessels, it not only gives up materials for the nourishment of the various tissues, but also has certain matters separated from it by structures termed *glands*, which may either be the channels for their immediate removal from the body, or the glands may transform them into substances of a different kind. Such materials separated by glands are called *secretions*, if they are destined to be of further use in the economy, and *excretions* if they are at once removed as waste products. Thus, saliva may be regarded as a secretion, whilst urine is an excretion. Strictly speaking, this is an arbitrary distinction, inasmuch as the two processes are practically identical. Urine is in the first instance secreted and afterwards excreted. Still, for practical purposes, it is important to distinguish between the two.

The anatomical conditions of secretion are essentially (1) a membrane more or less defined; (2) a layer of epithelial cells on one side of the membrane; and (3) bloodvessels on the other side. From these simple anatomical arrangements, as was first indicated by Sharpey, all the various forms of glandular structure may be evolved. This important generalization is illustrated by Fig. 117.

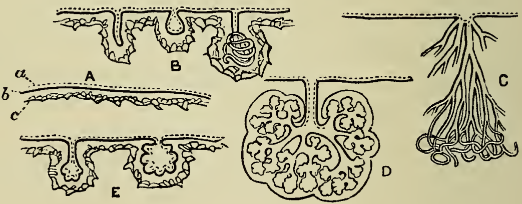


FIG. 117.—Anatomical arrangements of secreting structures. A. *a*, epithelium, composed of secreting nucleated cells; *b*, membrana propria, or basement-membrane; *c*, layer of capillary bloodvessels. B. Simple glands, straight tube to the left; sac in the middle; and coiled tube to the right. C. Compound tubular gland. E. Multilocular crypts, to the left, of a tubular form, and to the right, saccular. D. Racemose or compound saccular gland. The dotted lines represent the layer of epithelium.

The function of secretion is closely related to that of nutrition. Both depend, to a certain extent, as was first pointed out by John Goodsir, on the growth and development of structural elements. The older physiologists supposed that the elements of secretions previously existed in the blood, and that the process consisted essentially of the passage of these elements from the blood into the glands. Goodsir showed, by observations made on the cells of the ink-bag of the cuttle-fish, that the growth and development of cells played a most important part in the process. More recent facts have shown that the physical condition of blood pressure exercises a considerable influence, and that some of the elements of secretion are separated from the blood by a process of filtration, in which the propelling agent is the pressure of the blood. It is difficult to assign to each of these two elements its exact importance. Thus, in the secretion of saliva, Ludwig showed that the pressure in the salivary ducts might exceed that in the bloodvessels, and still secretion would go on; and, on the other hand, it has been proved that the separation of water from the blood by the kidneys is chiefly effected by the pressure of the blood in the capillaries of the Malpighian tufts.

The chief physical and chemical characters of the various secretions, are described in connection with each secretion, and the influence of the nervous system, as illustrated by what is known of the innervation of the salivary glands, has been described at p. 234.

Consult SHARPEY, art. Secretion, in Cyclopædia of Anatomy and Physiology; GOODSIR'S Anatomical Memoirs, edited by Turner, vol. II., p. 412; QUAIN'S Anatomy, vol. II., p. 231.

The various phenomena of elimination of waste matters by the tissues, and the formation and circulation of lymph have already been described, pp. 279-284, and the only stage in the process of nutrition still requiring discussion is that of excretion, by which matters hurtful to the tissues are separated by various channels.

VII.—EXCRETION.

Matters hurtful to the tissues are separated by five channels, namely, (1) the lungs; (2) the bowels; (3) the liver; (4) the skin; and (5) the kidneys. The lungs separate chiefly carbonic acid and aqueous vapour, as has been described at pp. 397-399; and the bowels separate excrementitious matters, as shown at p. 270.

A.—EXCRETION BY THE LIVER.

The general anatomical form and minute structure of the liver are described in all anatomical works. It consists essentially of a large number of minute lobules, each of which may be regarded as forming a liver in miniature. The various lobules are separated from each other by a thin layer of connective tissue forming a capsule, which is more or less marked in different species of animals. Each lobule receives a supply of blood from two sources, namely, (1) from the portal vein, and (2) from the hepatic artery. The first conveys blood to the lobule which has already passed through the capillaries of the stomach or intestines, and which is richly supplied with matters absorbed during its passage; whilst the second conveys arterial blood for the direct nourishment of the vessels, connective tissue, &c., of the lobule. From the blood of the portal vein, the hepatic cells in the lobule secrete various matters, some of which they pour into the origins of hepatic ducts, so as to form a fluid called *bile.* The blood is conveyed from the lobules by the origins of the hepatic vein, which vessel pours it into the vena cava. This blood has lost certain materials which have been separated from it to form bile, and it has gained other materials which have been elaborated by the hepatic cells. It will thus be seen that the functions of the hepatic cells are of a very complex character, inasmuch as they separate or form not only the elements of bile, but also are the seat of the changes which result in the formation of glycogen, sugar, diastasic ferment, urea, &c.

(a) *The Hepatic Cells.*—These are of a compressed spheroidal or polyhedral form, having a mean diameter of about the $\frac{1}{900}$th of an inch. They have no cell wall, but are composed of granular protoplasm in which a nucleus is imbedded. In the nucleus, two or more nucleoli may be seen, and there are frequently also small particles of fat or amyloid matter.

(b) *Origins of the Hepatic Ducts.*—These consist of fine intercellular passages forming a network between and around the individual cells. These minute bile ducts, according to Chrzonszczewsky,[1] are found chiefly on the flattened surfaces of the cells, the edges or borders being occupied by the blood capillaries.

Regarding the more minute structure of the liver, consult QUAIN, vol. II., p. 386.

The functions of the liver are as follows: (1) to form bile; (2) to form glycogen and a glycogenic ferment; (3) to form fat; and (4) it effects changes on blood corpuscles.

1. *Formation of Bile.*

The general physical and chemical characters of bile have been already described at p. 258. It is secreted under a low pressure, amounting in the cat to about 20 mm. of mercury. The secretion is constant, but it may not constantly flow into the intestine. In animals possessing a gall-bladder, it accumulates in this organ until the pressure in it overcomes the resistance at the opening of the common bile duct.

---

[1] Said to be pronounced as if written Chron-zin-dofsky.

Movements of the abdominal muscles also probably assist in its onward flow.

a. *Influence of the Circulation on the Secretion of Bile.*—The secretion is affected by changes in the amount of blood-pressure in the capillaries of the organ. Thus, it is increased by injecting blood into the veins, and it may be diminished by bleeding or by compression of the aorta. If the flow of blood through the portal vein be obstructed, the secretion diminishes or may be suppressed, and death speedily occurs. Again, the amount will be affected by the readiness with which blood flows away by the hepatic vein. An obstruction to the hepatic circulation first increases the secretion, but afterwards diminishes it. Ludwig and Schmulewitsch have succeeded in maintaining the secretion, for some time after removal from the body, by passing a stream of warm defibrinated blood through the liver of a rabbit. The influence of the circulation on the secretion of bile deserves more careful investigation, as a knowledge of the conditions might enable us to explain many pathological phenomena, such as congestions of the organ, and jaundice, occurring as consequences apparently of congested states of abdominal viscera.

b. *Influence of the Nervous System on the Secretion of Bile.*—Nothing definite is known regarding the influence of the nerves distributed to the liver on biliary secretion. The vaso-motor filaments are undoubtedly partly in the pneumogastric and partly in the splanchnics, so that section of the latter, or of the pneumogastric in the neck, is followed by congestion of the organ. Section of the vagi below the diaphragm is said to produce no effect. Pflüger states that he has seen secretion of bile continue after section of all the hepatic nerves. He also says that galvanization of the liver arrested the secretion. The whole of this department of nervous physiology is in obscurity, and merits investigation.

2. *Excretion of Bile.*

When the bile reaches the small intestine, it exercises, as pointed out on page 261, a comparatively feeble influence on the elements of chyme; but in the great intestine, at least a portion of it is decomposed, whilst the remainder is excreted unaltered in the fæces. The bile acids are split up into cholalic acid, glycocine, and taurine; and the colouring matter, bilirubin, is transformed into urobiline, which is reabsorbed to appear again as one of the pigments of the urine. It is probable, also, that the most of these substances are reabsorbed. Again, some of the bile acids may unite with neutral fats to form soaps, which are absorbed. It adds to the complexity of the transformations of the bile when we recollect that all the matters thus reabsorbed by the portal capillaries are conveyed back again to the liver, so that this organ appears to produce certain compounds which are thrown into the alimentary canal, there decomposed, their constituents reabsorbed, and carried back again to the liver, probably to form other compounds.

3. *Formation of Fat by the Liver.*

If we examine the hepatic cells of any of the domestic animals, especially those kept in confinement, fat globules are always seen in considerable numbers. Again, it is well known that in what is known to pathologists as *fatty liver*, the cells are filled with fat. This tendency to the formation of fat is probably connected with the production of glycogen. Thus, it has been supposed that glycogen in the liver may not only be transformed into sugar, but, in some circumstances, also into fat. If the fat be removed as quickly as it is formed, it may be oxidised in the tissues, or it may be stored up in the adipose tissue of some other organ; but if from interference with oxidation processes, it is not consumed, it apparently remains in the hepatic cells which become swollen, so that the aggregate size of the liver becomes increased. Thus there appears to be some kind of relation between oxidation changes, or, in other words, activity of respiration, and the formation of fat by the liver. In the embryo, and in fishes, where respiration is not very active, the liver is large; whereas in birds, which have an active respiration, the liver is very small. If a goose be kept from exercise, and fed with food rich in oils and carbohydrates in a hot and close atmosphere, the liver becomes fatty, increases enormously in size, and constitutes the *paté du foie gras* of Strasburg. We also observe similar changes, though to a less degree, in the liver of many residents in tropical countries, where they breathe a rarefied atmosphere, if they live on a rich diet and take too little exercise.

4. *Changes Effected by the Liver on Blood Corpuscles.*

Various facts indicate that in the liver there is a destruction or consumption of blood corpuscles. Thus if hæmoglobine be injected into the portal vein, there is an increased formation of bilirubin; and it has been supposed that the bile pigments are derived by the separation of $\underline{\underline{H}}$ from the coloured corpuscles. But what comes of the iron existing in $\underline{\underline{H}}$? It is not found in the hepatic substance, nor in the bile. It is possible, therefore, that in the liver, whilst old coloured corpuscles are decomposed, and their $\underline{\underline{H}}$ liberated, to be transformed partly into bilirubin, that at least a portion of the $\underline{\underline{H}}$ may be used in the manufacture of new corpuscles. In embryonic life, the liver abounds in colourless cells, and frequently nucleated cells are met with; and according to Lehmann, the blood of the hepatic vein is richer in corpuscles than the blood of the portal vein.

It must be confessed that our knowledge of the physiological changes in the liver is still very obscure. Evidently it is the seat of numerous chemical changes, of which the most apparent result is the formation of bile; but it is quite possible that the formation of this fluid may be less important than some other phenomena, such as the formation of glycogen, the manufacture of the diastase which transforms the glycogen into sugar, the production of urea or uric acid, or the development or destruction of blood corpuscles. Again, on considering the comparatively simple structure of a hepatic lobule, as revealed by the microscope, one cannot help thinking that all the processes going on in the liver may have some physiological correlation.

Consult LAUDER BRUNTON, Functions of the Liver, in the Handbook for the Physiological Laboratory, p. 495; also, BEAUNIS' Physiologie, p. 464. Regarding the action of drugs upon the liver, see Report by the Edinburgh Committee of British Medical Association, Reporter, HUGHES BENNETT; and the more recent elaborate researches by RUTHERFORD and VIGNAL, published in the Scientific Reports of the British Medical Association.

B.—EXCRETION BY THE SKIN.

The skin not only serves as a very efficient protective covering to the body, but is a most important organ, constantly excreting water, fatty matter, and salts. It is also the seat of what is termed *cutaneous respiration.* The epidermis, hair, and various appendages which grow from its surface, may, in addition to the special purposes they are fitted for, also be regarded as excretions.

1. GENERAL STRUCTURE OF THE SKIN.

a. The *Epidermis*, or scarf skin, forms the outer layer of the skin, and consists of epidermic cells, round below, compressed above, and flattened externally. It varies in thickness in various parts of the body, being thin over the lips and flexures of the joints, and thick where it is subject to pressure, as on the fingers and heels. On making a thin vertical section from without inwards, it is seen in the last situations to be composed of flattened epidermic cells adhering together. Below this, they are fusiform; and, between the papillæ or projections of the corium, they may be seen in various stages of formation. As they are pushed outwards, they undergo a chemical change, the walls being at first soluble, but afterwards insoluble, in acetic acid, undergoing a horny transformation.

b. The *Cutis* or *Dermis*, also called *Corium*, or leather skin, constituting the deeper layer of the skin, is composed of white and elastic fibrous tissues, which vary in different proportions in various parts of the surface. Where great elasticity is required, as in the axilla, the elastic tissue predominates; where resistance is demanded, as in the sole of the foot, there is a close meshwork of areolar tissue. It also varies in thickness in different parts of the surface, being thin and delicate over the prepuce and eyelids, and thick where pressure is necessary, as in the sole of the foot. It may thus vary from ·24 to 2·80 mm. (Henle). The cutis rests on a layer of subcutaneous fat, which gives symmetry and roundness to the figure; externally it exhibits a series of ridges or projections called *Papillæ*, which are imbedded in depressions of the cuticle. These vary in shape and size. They are large, more numerous, and conical, on the tongue, palms of the hands, and soles of the feet, their average length being $\frac{1}{100}$ of an inch, and breadth at the base $\frac{1}{250}$ of an inch. They are richly furnished with capillaries in the form of loops derived from an arterial twig from the arterial plexus. The vascularity is greatest where the ridges are most marked, and the sense of touch best developed. Hence the loops of nerves and bloodvessels are more numerous in the papillæ of the fingers than on the back of the hand. Some papillæ are only furnished with bloodvessels, others with nerves, and a third kind with both. They have been considered, therefore, as vascular and tactile, the former being most numerous. (*Allen Thomson.*)

c. The *Sudoriferous* or *Sweat Glands* lie at various depths in the true skin. They consist of a tube, blind and convoluted into a ball at its furthest extremity, which terminates externally on the surface of the cuticle. The tube is of the same diameter throughout, about $\frac{1}{1700}$th of an inch, runs a straight course in the corium, but, on passing through the epidermis, becomes spiral. In the first position, it is formed of a thin membrane, lined by epithelium; in the second, it has no distinct coat, the spiral portion being a mere groove or channel in the epidermis, the cells of which are twisted in various directions to form its walls, as was pointed out by Rainey. These glands are scattered abundantly throughout the whole skin, but are most numerous on the palms of the hands and soles of the feet. In these situations, according to Krause, there are 2736 in each superficial square inch. In the same space on the back of the hand there are 1500; on the forehead and neck, 1300; on the breast, belly, and arms, 1100; on the cheeks and thighs, from 500 to 600; and on the back, 400. Wilson estimates the number on the palm of the hand at 3520 per square inch.

2. RESPIRATORY FUNCTIONS OF THE SKIN.

In many amphibians and reptiles, such as the frog, cutaneous respiration is very active, and is necessary for their existence; but the process is carried on to only a small extent in birds and mammals.

1. *Absorption of Oxygen.*—The amount absorbed by the skin is to that absorbed by the lungs as 1 : 27, and it is always less than the amount of CO_2 exhaled.

2. *Elimination of* CO_2.—About 4 grammes are separated during 24 hours. The amount is increased by a rise of temperature and by muscular exercise.

3. *Elimination of Watery Vapour.*—It would appear that some aqueous vapour is separated by the skin in addition to the water of the sweat. Thus Röhrig collected from the skin of the arm 1·6 grammes per hour, and he estimated the amount separated in 24 hours as about 200 grammes.

3. EXCRETORY FUNCTIONS OF THE SKIN.

The sudoriporous glands secrete *sweat*, and the sebaceous glands an *oleaginous matter*.

a. *Sweat.*

It is a transparent colourless liquid, having a peculiar odour, which varies in different parts of the skin. Acid reaction : sp. gr. 1004. The amount separated in 24 hours may range from 700 to 2,000 grammes. When examined under the microscope, it may show a few squamous epidermic cells, derived from the skin, and perhaps a few crystals and oil globules.

1. *Chemical Characters.*—It usually contains about 1 per cent. of solids, the greater part of which consists of

mineral matters. Traces of urea have been detected, as also minute quantities of formic, acetic, butyric, propionic, and caproic acids. The following table shows the result of analyses made by various observers :—

In 1,000 Parts.	Favre.	Schottin.	Funke.
Water,	995·573	997·40	988·40
Solids,	4·427	22·60	11·60
Epithelium,	...	4·20	2·49
Fat,	0·013	...	...
Lactates,	0·317	...	...
Sudorates[1],	1·562	...	...
Extractive matters,	0·005	11·30	...
Urea,	0·044	...	1·55
Chloride of sodium,	2·230	3·60	...
Chloride of potassium,	0·024	...	...
Phosphate of soda,	Traces	1·31	...
Alkaline sulphates,	0·011		
Earthy phosphates,	Traces	0·39	...
Salts in general,	...	7·00	4·36

The first portions of sweat secreted are rich in fatty acids and the last in mineral salts. With prolonged sweating, the secretion becomes very feebly acid or even alkaline. Copious drinking increases the amount, more especially if the skin be exposed to a warm and dry atmosphere. As a rule, all circumstances, operating from within, which cause an increased flow of blood to the skin also produce sweating. The influence of psychical states, such as fear or joyous excitement, is often very marked, but the rationale of such effects cannot be given Many substances, such as iodine, iodide of potassium, alcohol, and succinic acid, and the odoriferous principles of certain plants, such as garlic, may be eliminated by the skin.

---

[1] Favre mentions an acid peculiar to sweat which he calls sudoric acid, the existence of which is doubtful. The cause of the acidity of sweat has not been determined.

2. *Conditions of the Secretion of Sweat.*—The secretion of sweat depends on: (1) the pressure of the blood in the cutaneous capillaries; (2) the activity of growth in the epithelial cells lining the sudoriferous glands; and (3) the innervation of the part. Any increase of pressure in the cutaneous capillaries increases the production of sweat. Nothing definite is known regarding the innervation of the sweat glands. Claude Bernard has seen profuse sweating on one side of the head and neck after section of the sympathetic in the neck; and physicians are familiar with the phenomenon of local sweating in many nervous affections.

3. *Removal of Sweat from the Surface of the Skin.*—If the secretion be limited in quantity, and if the surrounding atmosphere be not saturated with aqueous vapour, the watery portion of the sweat immediately passes into vapour, constituting what has been called insensible perspiration. But if the secretion be abundant, or if the atmosphere be already saturated, the sweat soon bedews the surface and trickles over the skin. It is evident that in both cases, the surface of the skin may become coated more or less with solid or fluid matters, and if this state be allowed to continue, the matters may seal up the mouths of the sweat ducts and thus interfere with their functions.

b. *Sebaceous Matter.*

This matter, secreted by the sebaceous glands, is oily, semifluid, and has a peculiar odour. A microscopical examination shows fat cells, free fat, squamous epithelial cells and tablet-shaped crystals of cholestrine. It contains about 30 per cent. of fat, which is composed of olein and palmitine, probably combined with alkalies. It also contains alkaline chlorides and phosphates, and alkaline earths. The *wax of the ear*, or *cerumen*, is a variety of sebaceous matter secreted by modified glands in the external auditory meatus. In

1,000 parts, there are, of water, 100; fatty matter, 260; substances soluble in water, 140; substances soluble in alcohol, 380; and an insoluble residue, 120.

In addition to being an excretion, sebaceous matter lubricates the hairs, and renders them less hygroscopic, and it also, to some extent, renders the epidermis impermeable to water.

4. THE EPIDERMIC APPENDAGES OF THE SKIN.

In various classes of animals, the epidermis may be modified to form structures of diverse appearance, such as hairs, nails, horn, hoof, quill, feathers, and scales. The comparative study of these structures is of the greatest interest, but the limits of this work will not permit of its discussion. The chief physiological points to be noted are: (1) each epidermic structure may be regarded as a permanent excretion from the blood; (2) each epidermic structure has an individual existence—it is developed, grows, reaches maturity, declines, dies, and is removed from the body to be replaced by another of a similar kind; (3) epidermic appendages of the most varied histological structure may serve purposes of beauty (hair, feathers, scales), of warmth (wool), of defence (horn, hoofs, quills or spines), or as aids to the sense of touch (whiskers of the cat and other felines, &c.); and (4) when epidermis is modified for purposes requiring strength and resistance, it assumes in structure a concentric arrangement of epidermic cells, simulating bone (contrast, for example, bone with sections of hoof, of whalebone, or of rhinoceros horn).

C.—EXCRETION BY THE KIDNEYS.

The substances separated from the blood by the kidneys consist essentially of water, various nitrogenous matters, and salts. Like other processes of excretion, the separation of these matters depends partly on the pressure of the blood, and partly upon the activity of certain cellular elements, found in the structure of the excretory organ.

On opening a kidney by a longitudinal section, from its outer to its inner border, the solid portion is seen to consist of a *cortical* and a *medullary* substance; the latter being in the form of conical masses named *Pyramids of Malpighi*, the points of which open into a space called the *sinus*. The cortical part is of a light crimson brown colour and is soft and easily lacerated. The urine is secreted chiefly in the cortical part, and it is conveyed by the medullary part into the sinus, from there into the *pelvis*, or dilated extremity of the ureter, and by the ureter it passes into the bladder. The kidney is richly supplied with blood vessels, lymphatics, and nerves.

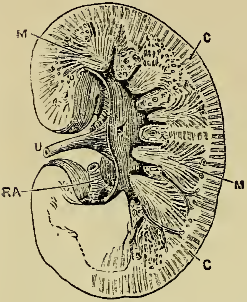


Fig. 118.—Section of a Kidney; *p*, sinus; *u*, ureter; *m*, medullary; and *c*, cortical part.

1. General Anatomical Arrangements.

The organs consist essentially of a number of very elongated tubes, termed the *tubuli uriniferi*. These are, in their course, partly straight and partly convoluted, the former arrangement prevailing in the medullary, and the latter in the cortical, portion. The tubules, when examined microscopically, are seen to consist of a basement membrane, lined by epithelium. The character of the epithelium is different in different parts of the same tubule. Thus, the epithelium is columnar in the larger tubules of the medullary portion and is of such a size as to leave a free and wide passage in the centre of the tubule; whereas in the cortical portion it is more cylindrical in shape, glandular, and so large as almost to fill the tubule. As already stated, the tubules in the cortical part of the kidney are very much convoluted, and those in the medullary part are straight. It was once supposed that those in the cortex, after winding about, ended in tubules which then pursued a comparatively straight course towards the pelvis of the kidney; but Henle showed that at least some of the tubules, when traced from the cortical portion, form loops extending into the medullary portion. These loops, forming the *looped tubules of Henle*, on returning to the cortical substance, again become convoluted, and ultimately terminate in tubules which pass directly into the medullary part. The part of Henle's loop which passes into the medullary part is small in diameter, and is lined by flattened epithelial cells, whilst the part returning to the

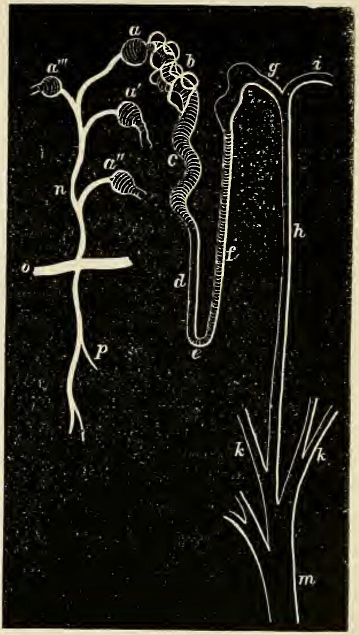


Fig. 119.—Diagrammatic view of the arrangement of the tubules in the kidney. *a*, Malpighian body; *b, c, d, e, f*, uriniferous tubule forming one of Henle's loops—observe the width of the tube at its commencement, that it becomes narrower and afterwards again becomes wide in the cortical part; *g*, canal joining it with *h*, straight tube of Bellini; *i*, a similar uniting canal; *k, k*, other tubes of Bellini; the shaded part of the tube is where the epithelium is glandular; *a′ a″ a‴*, other Malpighian bodies, connected with the arteriole *n*, which arises from larger artery *o*; *p* is a branch of *o* returning to the medullary part direct; the veins are not represented. They are very large. At *b*, observe the plexus on the tubule formed from the efferent vessel of the Malpighian body, *a*.

cortical portion is broader, and is filled with glandular epithelium to such an extent as almost to fill the lumen of the tube.

It would appear, therefore, from the researches of histologists, that if we traced a tubule from its origin to its termination, its course would be as follows: it arises by a capsular dilatation which surrounds a tuft of vessels known as a *glomerulus* in the cortex; from thence it passes into the medullary portion, forms a loop, and returns again into the cortical portion, where it joins, by a short canal, a straight tube called *a straight tube of Bellini*, and the latter pursues its course towards the apex of one of the pyramids, uniting, from time to time, with tubes of a similar character. The general arrangement is shown in diagram, Fig. 119. Secretion chiefly occurs in the tubules having glandular epithelium, the others being for the purpose of carrying away the secretion formed.

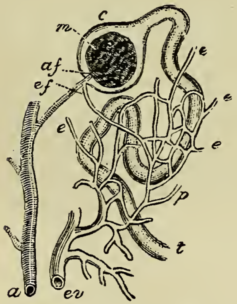


Fig. 120.—Diagram showing the relation of the Malpighian body to the uriniferous tubules and blood-vessels. *c*, expansion of the end of the tubule; *m*, tuft of vessels, forming glomerulus; *af*, afferent vessel, conveying blood to, and *ef*, efferent vessel, conveying blood from, *m*; the efferent vessel, *ef*, splits up into capillaries *e*, *e*, *e*, *e*, which ramify on the uriniferous tubule.

To understand the functions of the kidney, it is important to bear in mind the arrangements of the vessels. The branches of the renal artery split up into capillaries, which form an elongated meshwork in the medullary part, and an irregular meshwork in the cortical part. If one of the larger of these vessels be traced into the cortical portion, it will be found to terminate in what has for many years been known as a *Malpighian body*, as represented in Fig. 120.

A Malpighian body consists of a *glomerulus*, or tuft of vessels, enclosed by an expansion of the end of a tubule, as was first pointed out by Bowman. Each possesses an *afferent* vessel, which carries blood into it, and an *efferent* vessel, which carries blood away from it. The efferent vessel, usually smaller in calibre than the afferent, divides into a number of capillaries, which ramify upon the tubule, the dilated end of which forms the capsule surrounding the glomerulus. Thus in the kidney there are two capillary plexuses, one in the glomerulus, and the other in the plexus on the tubule. From a physiological point of view, it is important to recollect (1) the arrangement of the tubules; (2) the distribution of the vessels; and (3) the different forms of epithelium, that in the *secreting tubules* being glandular, whilst in the *conducting tubules* it is similar to what is found in the ducts of glands. According to Ludwig, also, the tubules are surrounded by lymphatic spaces which communicate freely with each other.

Consult regarding Structure of the Kidney, Bowman, Philosophical Trans., 1842; and Quain, vol. II., p. 402.

2. General Characters of the Urine.

The urine is a clear, transparent fluid, of an amber colour, peculiar odour, and saltish taste. Normal density, 1020; reaction, slightly acid, owing to the presence of acid phosphates of soda or uric acid. On microscopical examination, it may be found to contain a few epithelial cells. The average amount passed in 24 hours is from 40 to 60 ounces (about 1200 c.c.)

a. *Chemical Constituents.*

Normal urine contains about 960 parts of water to 40 parts of solids. The latter may be divided into four groups: (1) nitrogenous; (2) non-nitrogenous; (3) pigments; and

(4) saline matters. It also contains in solution a small quantity of gas.

1. *Nitrogenous Matters.*—These consist chiefly of urea and uric acid. In addition, there are small quantities of hippuric acid, creatine, creatinine, xanthine, &c. About 500 grains of urea and 7 of uric acid are excreted in 24 hours.

2. *Non-nitrogenous Matters.*—The urine is not rich in such matters; it may contain traces of fatty acids, such as acetic, butyric, and propionic; also taurylic and damaluric. Small quantities of oxalic acid and glucose may be present.

3. *Pigments*—These are indican and urobiline. Indican is sometimes present in such quantity that the urine becomes of a bluish colour after having been exposed to the air for several days. By oxidation, it may produce various indigo-pigments, such as indigo-blue, indiglucine, &c. Thus:—

$$\underset{\text{Indican.}}{C_{26}H_{31}NO_{17}} + 2\,H_2O = \underset{\text{Indigo-blue.}}{C_8H_5NO} + \underset{\text{Indiglucine.}}{3\,C_6H_{10}O_6}$$

From its chemical relations to leucine, tyrosine, and other products of the decomposition of albuminous bodies, the conjecture is that it may be produced in the alimentary canal. Urobiline, on the other hand, is derived from the pigments of the bile; which, in turn, as already stated, arise from the decomposition of hæmoglobine.

Vogel has classified the numerous varieties of shades of colour met with in urines thus: (1) yellow urines; (2) reddish urines; and (3) brown or dark urines. The varieties of colour do not depend on different pigments, but on different degrees of dilution of the two pigments above mentioned. Thus, on evaporating a light-coloured urine, it will be darker as it becomes more concentrated; and on the other hand, dilution with water of a dark urine causes it to pass through lighter and lighter shades.

4. *Inorganic Substances.*—These exist, in normal urine, to

the extent of 15 grammes to 1 litre. The 15 grammes are composed as follows: chloride of sodium, 10 grammes; phosphoric acid, 2 grammes; sulphuric acid, 1 gramme; and the remainder is constituted by potash, soda, lime, magnesia, and traces of iron and of silica.

5. *Gases.*—100 volumes of urine usually contain 14 volumes of gas, consisting of about 13 volumes of CO_2, 1 volume of N, and traces of O. Thus, it would appear that the kidneys eliminate small quantities of CO_2 and of N.

The following table, given by Vogel, shows, in the first column, the composition of urine in 24 hours; and, in the second, the composition in 1000 parts:—

	In 24 hours in grammes.	In 1000 parts.
AMOUNT OF URINE,	1500	1000
WATER,	1440	960
SOLIDS,	60	40
Urea,	35·	23·30
Uric Acid,	0·75	0·50
Chloride of Sodium,	16·50	11·00
Phosphoric Acid,	3·50	2·30
Sulphuric Acid,	2·00	1·30
Earthy Phosphates,	1·20	0·80
Ammonia,	0·60	0·40
Free Acid,	3·00	2·00

b. *Changes in Urine after Exposure to Air.*

When exposed to the air, it undergoes two changes, which have been termed fermentations.

1. *Acid Fermentation.*—When the urine has been left at rest, especially under the influence of a moderate degree of heat, its acid reaction becomes stronger; and distinct crystals of uric acid are often deposited on the sides and bottom of the glass. This increase of its acidity goes on for some days,

and may even continue in rare instances for two or three weeks. The acidity, however, at last begins suddenly to diminish, and gradually disappears.

2. *The Alkaline Fermentation.*—The urine now becomes lighter in colour; a whitish, iridescent pellicle forms on its surface; and the presence of ammoniacal odour indicates that it has become alkaline. A deposit is thrown down, consisting of the ammoniaco-magnesian or triple phosphate, phosphate of lime, and urate of ammonia. This change, the alkaline fermentation, is owing to the decomposition of urea into carbonate of ammonia. Urea unites with the elements of water thus:—

$$\underset{\text{Urea.}}{CN_2H_4O} \quad + \quad 2(H_2O) \quad = \quad \underset{\text{Carbonate of ammonia.}}{(NH_4)_2CO_3}$$

The urine is thus rendered alkaline, and the earthy phosphates, being insoluble in alkaline fluid, are precipitated—the phosphate of lime as such, and the phosphate of magnesia as the triple phosphate of ammonia and magnesia ($MgNH_4PO_4 + 6H_2O$).

c. *Changes in the Urine in different Physiological States.*

1. *Age.*—Considering the weight of the body, an infant secretes more urine, and more urea and salts, than an adult. In the aged, the quantity and the solids are much diminished.

2. *Sex.*—The female secretes less urine, and the proportion of solids is also less, than the male.

3. *Nature of the Diet.*—Fluids not only increase the quantity of water, but also the amount of salts, but they do not appear to affect the quantity of urea and uric acid. A rich animal diet increases the quantity of urea, uric acid, sulphates, phosphates, and chlorides; a vegetable diet makes the urine alkaline, as in herbivora, and it increases the amount of hippuric, oxalic, and carbonic acids, united with

the alkalies and alkaline earths. Starvation of a herbivorous animal causes the urine to become acid, and to resemble in constitution that of a carnivorous animal.

4. *Influence of Digestion.*—About three hours after a full meal, the urine becomes dense, highly coloured, and contains a large quantity of solid matters, the nature of which will depend upon the kind of diet. It may also then be alkaline.

5. *State of the Skin.*—When the action of the skin is increased, as by cleanliness, exposure to a warm and dry atmosphere, or by the use of special drugs called diaphoretics, the amount of water separated by the kidneys is diminished. The reverse is also true. It is important to note, however, that the correlation between the functions of the skin and of the kidneys influence chiefly the water, and only to a very slight extent the solid matters.

6. *Muscular Exercise.*—This may increase to a slight extent the amount of urea excreted, a statement which will be illustrated in treating of the elimination of that substance.

7. *Sleep.*—The urine passed in the morning is usually dense, highly coloured, and more strongly acid than at any other period of the day. The water is diminished, a fact which may probably be explained by the increased activity of the skin during the night. It is stated that urea, chloride of sodium, and sulphates are also diminished, and that phosphates alone are increased.

8. *Pregnancy.*—During this state, the urine is often high coloured and dense, and shows on the surface a pellicle, called *kyestine,* of an iridescent appearance and a peculiar odour. When examined microscopically, it is found to consist of numerous crystals of the triple phosphate, molecular matter, bright refractive particles like those of fat, and possibly minute *torulæ* or other microscopic organisms.

d. *Changes in the Urine produced by External Causes.*

1. *Diurnal Variations.*—Various observers have noticed distinct variations in the amount and composition of the urine at tolerably fixed periods in each stage of 24 hours. Thus, chloride of sodium presents two maxima, the one in the morning and the other after mid-day; uric acid also two maxima, the first at 7 a.m. and the other at 5 p.m.; sulphates reach a maximum about six hours after a meal; and the phosphates reach a maximum about 7 p.m., and fall during the night. In considering these variations, it must be remembered that at least two factors may contribute to the result: (1) the amount of the substances introduced in the food; and (2) the amount of disassimilative changes occurring in the tissues. We would therefore expect that substances introduced in the food would reach their maxima after a time required for their digestion, assimilation, and excretion by the kidneys; and that those which resulted from waste of tissue would be at a minimum during the periods in which little waste was going on, as, for example, in the night.

2. *External Temperature.*—A warm temperature diminishes the quantity of urine, and makes it more concentrated, probably by increasing the activity of the skin.

3. *Changes caused by Drugs.*—By the term drug is not necessarily understood a substance employed in medicine, but any substance having a physiological action on an organ or tissue. Most mineral matters introduced with the food are excreted by the kidneys in the same state; but there are exceptions. Thus iodides are converted into iodates, and ferricyanides ($K_3Fe_2Cy_6$) into ferrocyanides ($K_4Fe_2Cy_6$). Organic acids usually undergo change. Malates, tartrates, &c., are converted into carbonates; tannates into gallates; and benzoic into hippuric acid. Many colouring matters,

such as turmeric and madder, and many odoriferous matters, such as that of oil of turpentine, pass through unchanged. Santonine gives the urine the colour of saffron. Some active substances probably increase the quantity of urine excreted by influencing the amount of blood pressure; whilst others may possibly have a specific effect on the secreting cells of the tubules.

3. Elimination by the Kidneys of Nitrogenous Matters.

In addition to the separation of water and saline matters, one of the most important functions of the kidneys is the elimination of nitrogenous matters, chiefly in the form of urea and uric acid.

a. *Elimination of Urea.*

About 30 grammes of urea are excreted during twenty-four hours. This amount depends chiefly on the nature of the diet. A diet rich in albuminates increases, whilst one consisting chiefly of fats and carbohydrates diminishes, the amount of urea. Much controversy has taken place as to the influence of muscular exertion. Liebig supported the view that muscular activity was carried on at the expense of nitrogenous matters obtained either from the muscles themselves or from the food. According to this view, he divided foods into *tissue-forming*, such as albuminates, and *heat-producing*, such as carbohydrates and fats. The first he supposed were used for the construction of the tissues, and for the production of muscular work; whilst the second, by oxidation into carbonic acid and water, were regarded as the producers of heat. It is well known that the chief products of the decomposition of nitrogenous matters are urea and uric acid; whilst those resulting from non-nitrogenous matters are carbonic acid and water. If, therefore, the theory of Liebig were true, we would expect to find that prolonged muscular exercise would cause an increase in the amount of urea and uric acid separated by the kidneys. This question has repeatedly been put to the test of experiment, more especially by Voit, Parkes, Flint, and Fick and Wislicenus. The observations made by the latter, Fick and Wislicenus, both expert physiological chemists, are generally regarded as conclusive. These two observers, in 1866, ascended the Faulhorn, one of the Swiss Alps, about 1,956 metres high. For seventeen hours previous to the ascent, they took no nitrogenous food; the ascent occupied six hours; and for six hours after the end of this period, they lived on starch and sugar. The urine passed was collected and examined. It was collected in four portions, each of which was separately examined: (1) before the ascent; (2) during the ascent; (3) during six hours of repose after the ascent, at the end of which time they had a meal rich in nitrogenous matter; and (4) during the night passed on the mountain after this meal. It will be observed that the amount of work produced during the ascent must have resulted either from changes in their albuminous tissues, or been derived from the non-nitrogenous matter used in their food. By thus collecting and estimating the urea formed, and assuming that it was all produced from albuminous matter, it was not difficult to calculate the amount of albuminous matter represented by this quantity of urea, and the amount of energy liberated by the oxidation processes. The actual amount of energy, in the form of muscular movement, expended during the ascent was ascertained by multiplying the body-weight by the height. Thus, the work done by Fick was 66 kilos. × 1,956 = 129,096 kilogrammetres, and that of Wislicenus was 76 × 1,956 = 148,656 kilogrammetres. But the amount of energy liberated by the presumed decomposition of albuminous matters was found in the case of Fick to be only 66,690 kilogrammetres, and of Wislicenus only 68,376 kilogrammetres—both little more than one-half of the energy actually expended. It was evident, therefore, that the energy expended could not have been entirely obtained from the decomposition of nitrogenous matters, and that the amount of urea was not, as Liebig had supposed, any measure of the muscular waste. The following brief table gives the amount of nitrogen in the urea excreted in the different periods:—

Urine.	Fick.		Wislicenus.
	Grammes of Nitrogen in the Urea.		
1. During period of 17 hours previous to the ascent, ...	6·9	...	6·6
2. During 6 hours occupied by ascent, .	3·3	...	3·1
3. During 6 hours of repose after ascent,	2·4	...	2·4
Full Nitrogenous Meal.			
4. During the night spent on the mountain after the meal, . . .	4·1	...	5·3

On studying these facts, it will be observed (1) that the amount of nitrogen excreted was very much lessened by the non-nitrogenous diet, even during the ascent and during the period of repose, when muscular waste might be supposed to have been going on; (2) that the amount of nitrogen was increased immediately after a nitrogenous diet; (3) that the energy actually consumed during the ascent was much greater than could be accounted for by presumed changes in nitrogenous matter, estimated from the amount of urea excreted; and (4) the inference is that muscular energy is at least partly derived from changes occurring in carbohydrates and fats, and not, as Liebig supposed, from changes in nitrogenous tissues alone. These researches have been corroborated by Pettenkofer and Voit, who have shown that the amount of carbonic acid is largely increased during muscular exercise, exactly what would be expected if we assume that, during muscular work, carbohydrates and fats are chiefly used. Various somewhat contrary results as regards the amount of urea excreted have recently been obtained by Flint in observations on Weston, the famous pedestrian, but the discrepancies cannot at present be accounted for.

When urea is prevented from escaping, a condition termed *uræmia* is the result. It frequently occurs in the later stages of diseases of the kidneys, and in the course of fevers. The individual passes into a state of profound coma, and convulsions may terminate life. Frequently, in these cases, the skin is bedewed with a dark-coloured sweat, having a urinous odour.

b. *Elimination of Uric Acid.*

About ·5 grms. of uric acid are separated daily. It is said to be slightly increased by muscular work. According to Ranke, it is at a minimum in the morning, and the amount increases after a full meal. It exists principally in combination with bases, forming urates of soda and potash. Sometimes in normal urine, there may be traces of urate of lime, and in decomposing urine there is always urate of ammonia. Alkaline urates are much more soluble in hot than in cold water, and consequently, where they are in excess, as in febrile conditions, they are precipitated as an amorphous substance, when the urine becomes cold. The application of heat causes their re-solution. Uric acid is produced by the oxidation of nitrogenous matters. It contains less oxygen than urea, and it is transformed into urea in the body. It may probably be regarded as a residue of some intermediate substance not fully oxidised. In birds and serpents, the oxidation process seems to be arrested, and the result is the appearance of large quantities of urates and of free uric acid in the urine. Any constitutional state which interferes with oxidation, or with the elimination of uric acid, may produce excess of this substance. The excess may be so great that an equivalent amount of bases is not separated, and the result is the appearance of crystals of uric acid in the urine, constituting the *uric acid diathesis.* In such circumstances, also, urates may be deposited in fibrous structures in the vicinity of joints, giving rise to local affections, and a constitutional state called *gout.* When uric acid is excreted in excessive quantity, it is liable from its insolubility, to form concretions or calculi in the pelvis of the kidney or in the bladder. Excessive excretion of oxalates may produce the same effect. In the bladder, these concretions may become coated with deposits of phosphates, constituting calculus or *stone.* When minute particles or grains appear in the urine, they receive the name of *gravel.* In the urine of herbivora, hippuric acid occupies the place of uric acid.

c. *Elimination of Albumen.*

Albumen is sometimes met with in small quantities even in healthy urine. It may do so after a meal very rich in egg-albumen, or after copious draughts of water. In such cases it is transient; but when permanent its appearance is indicative of serious disease. The principal causes which determine *albuminuria* are: (1) diseases of the kidneys, causing changes in their vessels or in the secretory epithelium; and (2) derangements of the circulation, such as diseases of the heart, lungs, liver, or systemic arteries, which so present obstructions to the passage of blood as to cause a great increase of blood pressure.

4. Mechanism of the Secretion of Urine.

It is important to remember that the kidneys are supplied with blood, through the renal arteries, directly from the arterial system; that the blood is conveyed from them by renal veins, which empty themselves into the inferior cava, and that they are also richly supplied with lymphatics. During its passage through the organs, the blood loses certain materials which constitute urine, which is conveyed from the kidney to the bladder by the ureters. This loss might possibly result from a simple process of transudation from the blood, or from activity of epithelial cells, or from both together. Numerous experiments and observations have shown that the secretion is always increased with an increase of blood pressure. It has been observed that the secretion ceases when the pressure is such that the renal venous circulation becomes very slow. Ligature of the ureter at once stops the secretion, and any influence which tends to increase the pressure in the ureter has the same effect. It would thus appear that the secretion depends partly upon difference of pressure in the vessels of the kidney and in the ureter. If the pressure in the kidney be much increased, more urine will be secreted; and the reverse holds good. The state of the blood has also a certain influence. Thus an increased quantity of water, introduced as drink, by simply increasing the blood pressure, is followed by a larger excretion of water. From the anatomical arrangements of a Malpighian body, and especially from the fact of the efferent being smaller in calibre than the afferent vessels, it is evident that the pressure in the vessels forming the glomerulus must be greater than in the general capillaries. If so, water from the blood will be separated in the Malpighian body by a simple process of filtration under pressure, and will fall into the dilated end of the uriniferous tubule. On the wall of this tubule, as already stated on p. 454, capillaries formed from the efferent vessel are distributed, and from the blood contained in these the epithelial cells in the tubule probably secrete the solid elements in urine. It is difficult to conceive, however, that only water is separated in the glomeruli, as in the physical conditions assumed to exist, crystalloids, such as the various salts, would also pass. If so, the epithelial cells probably contribute nitrogenous matters and possibly pigments.

The excretion of urine becomes somewhat more complicated when the presence of the lymphatics is taken into account. Ludwig has shown that the tubuli are surrounded by lymphatic channels, and he has pointed out that interchanges probably take place between the lymph and first secreted urine. According to his theory, blood pressure plays the principal part; under its influence, the serum of the blood, less the fats and albuminates, filters through the walls of the capillaries of the glomerulus. Then it is brought into contact with the epithelium of the tubes and the lymph in the channels surrounding the tubes; and some matters may be re-absorbed from the fluid in the tubules by the lymph, and possibly by the blood in the capillaries of the efferent vessel. It appears to the author that in Ludwig's theory, he does not attach sufficient importance to the activity of the epithelium lining the tubes. In the positions where elimination would probably take place, as in the tube at its origin, and in the descending limb of Henle's loop, the epithelium is distinctly glandular; whereas, in the other portions, it has more of the appearance of protective epithelium, which may secrete mucus, as found in the ducts of all glands. The secretion of urine, therefore, depends upon the following conditions: (1) the anatomical arrangements for producing local increase of blood pressure; (2) circumstances causing increase in the general blood pressure; (3) circumstances affecting pressure in the lymphatics of the kidney; (4) circumstances affecting pressure in the larger ducts, pelvis, and ureters; and (5) the activity of the epithelium lining the smaller tubules.

5. INNERVATION OF THE KIDNEY.

Little is known as to the exact influences of the central nervous system on the secretion of urine. Section of the spinal cord in the cervical region arrests the secretion, probably from lowering of the blood pressure in consequence of general vaso-motor paralysis. Section of the splanchnics is said to increase the secretion, whilst stimulation of the distal end augments it, an effect likely to be produced if we suppose that this nerve contains the vaso-motor filaments supplying the vessels of the kidney. Whilst there can be no doubt that the cerebral centres may affect the secretion of urine, as evidenced by the well-known results of emotional conditions, the channels by which the influences pass are unknown.

6. EXPULSION OF URINE FROM THE BLADDER.

The urine is secreted constantly by the kidneys, is forced along the ureters by the pressure of secretion, and is discharged into the bladder drop by drop. This phenomenon has actually been seen in some cases of congenital malformation, in which the anterior wall of the bladder and of the abdomen are deficient, so as to expose the openings of the ureters. It is probable that the urine is partly propelled along the ureters by rhythmical muscular contractions occurring in their walls. The bladder slowly fills, in consequence of the urethral orifice being firmly closed. Up to a certain limit, the closure of the urethral orifice is involuntary and unconscious, and it probably is due to a contraction of involuntary muscular fibres forming a kind of sphincter in the prostatic portion. In the female urethra, where the prostate does not exist, the occlusion must depend upon some such action; but probably, in the male, the elasticity of the prostate may assist. When the bladder reaches a certain degree of tension, the sensory nervous filaments in its walls are affected so as to give rise to a sense of fulness. A slightly greater distension apparently causes reflex contraction of the muscular fibres near the neck of the bladder, which forces a few drops of urine into the prostatic portion. When this occurs, the desire may become so strong as scarcely to be resisted; and after a short time, reflex contractions occur in the wall of the bladder, which, assisted by voluntary contractions of the abdominal muscles, expel the urine. The locality of the reflex centre which governs these mechanisms has not been precisely fixed, but it is undoubtedly in the lumbar region of the spinal cord. Disease of this portion of the cord is attended by incontinence of urine.

Consult, as the best work on the chemistry of the urine, NEUBAUER and VOGEL'S Treatise translated by the Sydenham Society; also, LAUDER BRUNTON in Handbook for Physiological Laboratory, p. 532. Regarding the mechanism of secretion, see LUDWIG'S article in Wagners' Handwörterbuch der Physiol.; also, BOWMAN in Philos. Trans. 1842. A full critical description of the various theories of urinary secretion is also given in WUNDT'S Physiologie, p. 339.

VIII.—EXCHANGE OF MATERIALS.

Having now considered the various processes occurring in the great function of nutrition, by which all the tissues are supplied with materials for their nourishment and growth, and for the due performance of their functions, and by which the waste matters resulting from activity of tissue are removed, it is important to attempt to ascertain what relation exists in a healthy adult between the ingesta and the excreta. By *ingesta* are meant all the materials introduced into the body, either by the lungs, skin, or alimentary canal; whilst the term *excreta* signifies the matter thrown out by the various excretory channels. If we suppose the weight of the body to remain the same, it is evident that the ingesta would be exactly equal to the excreta; if at the end of the experiment, the body showed an increase of weight, the ingesta would be in excess of the excreta; and *vice versa.*

In studying this view of the phenomena of nutrition, it is necessary to know the weights of the various tissues and organs forming the body. This can only be done approximately; but it has been attempted by Bischoff and Krause, who have given us the following table showing the weight in grammes of the anatomical elements of a body.

	Grammes.
Muscles and tendons,	35,158
Fresh skeleton,	9,753
Skin and adipose tissue,	7,404
Blood,	1,500
Liver,	1,856
Brain,	1,430
Lungs,	1,200
Small intestine,	780
Great intestine,	480
Great vessels,	361
Kidneys,	292
Heart,	292
Nervous trunks,	290
Spleen,	246
Stomach,	202
Bladder and penis,	109

	Grammes.
Pancreas,	88
Tongue and its muscles,	83
Larynx, trachea, and bronchi,	79
Æsophagus,	51
Parotid glands,	50
Spinal cord,	36
Testicles,	36
Submaxillary glands,	18
Prostate,	18
Eyes,	15
Thyroid glands,	15
Supra-renal capsules,	11
Thymus,	7
Sublingual glands,	6

These figures are merely to be regarded as approximates. No organ in two or more individuals would probably have the same weight, and each organ varies in weight at different times in the same individual.

Many experiments have been made upon the lower animals, chiefly upon dogs, in which the ingesta or excreta have been carefully weighed, and the body of the animal has also been ascertained, from time to time. In such experiments, arrangements were made for collecting the gases given off in respiration, as well as the matters voided by the skin, kidneys, and bowels. It would manifestly be extremely difficult to carry out such an experiment with strict accuracy, in the case of a human being; and accordingly, the following table given by Vierordt, in which he states in grammes the amount of income and expenditure of the organism in a healthy man in twenty-four hours is only approximative. He has collected the data from the record of numerous experiments made by different physiologists upon different individuals, and the figures stated can only be regarded as approximative mean quantities, and nothing more. [1]

I.—INGESTA.

	C.	H.	N.	O.	Total.
Oxygen inspired, .	...	...	...	744·11	744·11
Albuminoids, . .	64·18	8·60	18·88	28·34	120·0
Fats, ...	70·20	10·26	...	9·54	90·0
Starch, ...	146·82	20·38	...	162·85	230·0
Water, ...	...	...	...	...	2818·0
Salts, ...	...	...	...	...	32·0
Total ingesta, . .	281·20	39·19	18·88	944·84	4134·11

---

[1] It would serve no useful purpose for the student to burden his memory with these figures. They are given for reference, and to illustrate the general principle of a balance, as regards matter, being struck in the economy of the body.

II.—Excreta.

	Water.	C.	H.	N.	O.	Salts.	Total.
Lungs, . .	330	248·8	...	...	651·15[1]	...	1229·9
Skin, . .	660	2·6	...	...	7·2[1]	...	669·8
Kidneys, . .	1700	9·8	3·3	15·8	11·1	26	1766·0
Bowels, . .	128	20	3·0	3	12·0	6	172·0
Water formed in the body,	...	...	32·89	...	263·41	...	296·3
Total Excreta,	2818	281·2	39·19	18·8	944·86	32	4134·0

From this table, it will be observed: (1) that in alimentation the nitrogenous principles are to the non-nitrogenous in the proportion 1 : 3·5; (2) that of the total eliminated products, the lungs separate 32 per cent., the skin 17, the kidneys 46, and the bowels about 4·5 per cent.; (3) that the amount of the various elements in the first table are exactly equal to the amount of the same elements in the second table; and (4) that the totals in both tables also correspond.

If, in a healthy organism, doing both *external* work, say mechanical labour, and *internal* work, in carrying on circulation, respiration, &c., the amount of matter introduced be not equal to the necessities of the vital and physical conditions in which it lives, it is evident either that the activity of the system will be diminished, or that materials will be used up which had been previously stored in the body, or, in other words, that the evolution of energy and the changes of matter will take place at the expense of tissue. Each organism is capable of carrying on operations for a certain time, although

---

[1] The whole of the O here mentioned is combined with the C to form CO_2.

the supply be considerably less than the demand, but at last a minimum limit is reached, beyond which the efficiency of the system will be impaired. On the other hand, there is probably a maximum limit of nutrition, that is to say, a point beyond which, in a particular organism, any excess of ingesta is never assimilated, but is simply thrown out in much the same state as when introduced. These limits cannot be strictly ascertained in the case of any individual man, and most persons roughly ascertain it for themselves by experience. Physiologists have been able to arrive at the general principle by careful observations made on dogs; but the results, in the hands of different experimentalists, have been on the whole so precise as to warrant the inference that in the human being also there is the same constant ratio between the matters introduced and the matters excreted.

During starvation, matters still continue to be eliminated, at the expense of the substances previously stored up in the economy. For a short time after the deprivation of food, a well-nourished organism may eliminate not very much less urea and carbonic acid than before; but the amount of these substances afterwards diminishes, and the weight of the body and of the excreta also rapidly fall off. Organisms rich in fat endure abstinence for a long time, and the deposit of fat disappears. When this has been used up, the muscles may next undergo fatty changes; and in course of time the skin, bones, liver, intestinal canal, and, lastly, the nervous system, undergo waste. The consumption of the materials of the body may in this way proceed to such an extent during starvation, that, at the death of the animal, it may have lost a little more than half the weight of the body at the commencement.

Hitherto the gain and loss of matter only have been discussed. In like manner, a similar balance might be struck between the income and outcome of energy, but this will be attempted after the consideration of the phenomena of animal heat.

Consult WUNDT'S Physiologie, p. 344; PETTENKOFER and VOIT, Zeitschrift f. Biologie, vol. II.; FICK and WISLICENUS, Züricher Vierteljahrschrift, 1865; PARKES' Papers in Proceedings of Royal Society, XV. and XVI.; FLINT'S Account of Experiments on Weston, 1877; and Article Nutrition, by MICHAEL FOSTER, in Watt's Dictionary of Chemistry, where a full historical development of the subject is given. See also Art. Nutrition in the supplement to the same work, where the results of observations by FRANKLAND, PARKES, &c., are detailed. The subject is also treated very fully in MICHAEL FOSTER'S Textbook of Physiology, in chap. V., on the Metabolic Phenomena of the Body.

INNERVATION.

Functions of Peripheral Nerves—Spinal Nerves—Cranial Nerves—Sympathetic Nerve—Nerves of Special Sense—General Functions of Centres—Spinal Cord—Medulla Oblongata—Basal Ganglia—Cerebellum—Cerebrum—General Conditions of Sensory Impressions—Touch—Taste—Smelling—Vision—Hearing—Voice—Speech.

The general phenomena of nervous action have been already described (p. 149 and p. 173). The nervous system, as there stated, consists of nerves, terminal organs, and centres. It has been pointed out that nerves are essentially conductors, that terminal organs are recipients, and that in the centres changes may occur which result either in motion, control of vessels or of glands, restraint of the activity of other centres, or in psychical phenomena, such as sensation, perception, feeling, volition, intellectual acts, and will. In the preceding pages, also, numerous illustrations have been given of the influence of the nervous system upon other great functions, such as the innervation of the digestive organs, of the heart, liver, &c.

The general structure of nerves will be understood with the aid of the following figure and of the description given at p. 151.

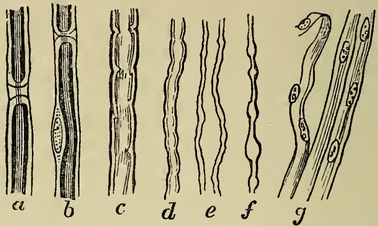


Fig. 121.—Nerves: *c*, ordinary-sized nerve-tube, showing axis cylinder surrounded by white substance; *d*, smaller nerve-tube, with white substance scarcely visible; *e*, still smaller, with no white substance visible; *f*, varicose nerve-tube, from grey matter near surface of brain; *a*, nerve-tube, coloured by *perosmic* acid, showing one of the *nodes of Ranvier*, or complete interruption of the white substance; *b*, nerve-tube showing nucleus and node of Ranvier (the axis cylinder is blackened by the action of the perosmic acid); *g*, non-medullated nerve-tubes from sympathetic, having no white substance, and nucleated at intervals.

The nerve centres are composed essentially of nerve fibres, various forms of nerve cells, and a delicate variety of connective tissue called neuroglia. The various forms of nerve cells are represented in Fig. 122, and a description is given in p. 150.

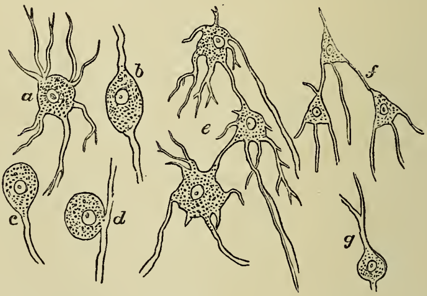


Fig. 122—Various forms of Nerve-cells: *a*, *multipolar*, from grey matter of spinal cord; *b*, *d*, *bipolar*, from ganglia on posterior roots of spinal nerves: *c*, *g*, *unipolar*, from cerebellum; *g* shows indications of a process coming off at lower end; *e*, union of three multipolar cells in spinal cord; *f*, union of three *tripolar* cells in grey matter of cerebral hemispheres.

Before proceeding to discuss the physiology of the nervous system, we may here point out the methods by which physiologists have acquired the information they now possess. In elucidating any problem in innervation, say the functions of a nerve, or the mode of action of a particular nerve centre, four lines of evidence are brought to bear upon the question, namely: (1) the inferences derived from *anatomical* examination of the origin, course, distribution, and general relations of the part, and the gradual development of the organ in the animal kingdom; (2) the facts derived from a careful examination of the *histological* structure of the part; (3) the *clinical* results observed by physicians, surgeons, and pathologists of the changes produced by diseases affecting nerves and nerve centres; and (4) the *experimental* facts observed by the physiologist when he cuts a nerve or nerve centre and stimulates the parts exposed. For many years, knowledge chiefly depended on the first and third of these modes. Certain nerves were traced to muscles and they were presumed to be motor; others were found in connection with the organs of sense and they were therefore held to convey sensory impressions; or an organ, such as the cerebrum, was found to increase in size and in complexity from the lower to the higher forms of vertebrates—(in animals of low intelligence, the brain was small and simple whilst it was large and complex in those of high intelligence)—the inference being that the cerebrum was somehow related to mental activity. Again, these inferences were corroborated by the observations of the physician and surgeon on man. Thus, when a certain nerve was cut in a surgical operation, the parts supplied were found to have been removed from the influence of the will or to have lost sensibility; tumours pressing on certain portions of nerve centres produced paralytic symptoms of various kinds; hemiplegia or paralysis, say of the left side, was found, on post-mortem examination, to be frequently caused by a clot of blood in the right brain, and *vice versa*. Still, such observations left much that was uncertain and obscure. Then the experimental method, in the hands of such men as Sir Charles Bell, John Reid, the Webers, Claude Bernard, and Brown-Séquard, threw new light on many obscure questions. They exposed a nerve, cut it, and observed the results. They then stimulated each end, say by a weak electric current, and noted the effect. If muscular movements followed, the nerve was held to contain motor fibres; or if pain was the result, it had sensory fibres in its course. By such methods also, our knowledge of the functions of the great cranial nerves, of the roots of the spinal nerves, of the influence of the nervous system on the heart, the lung, the liver, and the stomach has been rendered precise and accurate. Again, the experimental method has given much information regarding nerve centres. It is true that here, from the importance to the economy of the parts involved, from the influence of shock caused by the operation, and from our comparative ignorance of the structure of the parts, the results of the experimental method are less satisfactory. Lastly, the histological method, more especially as to the structure of the centres and of the terminal organs, has in recent years added much to our knowledge. It is the youngest of all the methods and has still much to do. There is still much to be acquired regarding the terminal organs, and more as to the topographical histology of the brain. It may be stated generally that when any theory regarding the physiology of a nervous organ is supported by evidence derived from each of these lines of enquiry, it may be accepted as true; but if it be contradicted by one or more, there is a fallacy to be discovered. Thus, the anatomist, histologist, physician, surgeon, pathologist, and physiologist are all engaged in the great work of unravelling the intricacies of nervous mechanism, a work which cannot fail to have important influences in the future, as it has had in the past, on the diagnosis and treatment of nervous diseases.

I.—FUNCTIONS OF THE PERIPHERAL NERVES.

Nerves originate from centres such as the spinal cord and brain, and ramify in all directions throughout the body. To distinguish them from the nervous cords or tracts which unite various portions of the nerve centres with each other, they may be termed *peripheral*, and for convenience may be classed as spinal, cranial, and sympathetic. In many classifications, the sympathetic nerves are kept entirely distinct from those termed cerebro-spinal; but it will be seen that there are the most intimate connections, both anatomical and physiological, between the two. The nerves issuing from the cerebro-spinal axis may also be divided into motor and sensory; and those found in connection with the terminal organs in the eye, ear, &c., are known as nerves of special sense. In considering nerves, we shall divide them as follows: (1) spinal nerves; (2) cranial nerves; (3) sympathetic nerves; and (4) nerves of special sense. Having described these, we will be in a position to consider the functions of the centres with which they are connected.

A.—FUNCTIONS OF THE SPINAL NERVES.

The spinal cord gives origin in its course to thirty-one pairs of spinal nerves, each nerve having two roots, *anterior* and *posterior*, the latter being distinguished by its greater thickness and by the presence of an enlargement called a ganglion, in which are found numerous bi-polar nerve-cells.

The fibres forming these roots may be traced into the cord, and their distribution will be considered in treating of that structure. The fibres of the two roots become intimately mixed with each other, so as to form the common trunk of the nerve at a very short distance beyond or close to the ganglion. The important discovery that these roots have different functions, that the fibres of the anterior root are *motor* and those of the posterior *sensory*, was made by Sir Charles Bell in 1811. This discovery was founded chiefly upon an experiment made by Bell, in which he found that irritation of the anterior roots of the spinal nerves in an animal shortly after death caused contractions of muscles, whilst irritation of the posterior roots produced no effect. In 1822, Magendie showed that irritation of the posterior roots caused pain. In some experiments made on warm-blooded animals, irritation of the peripheral end of the anterior root may cause not only contractions in the muscles, but also indications of pain. These indications of pain may still continue even after division of the mixed nerve beyond the fusion of the roots, but they cease at once on division of the posterior root. From this it has been inferred that some sensory fibres coming from the posterior root may form a loop into the anterior root, and then pass along the mixed nerve. By applying the method of Waller, described at p. 156, these looped fibres have been traced by degeneration occurring after separation from the ganglion.

Consult CHARLES BELL'S works on the Nervous System. The first indication of Bell's views is given in a tract printed in 1811, entitled "Idea of a New Anatomy of the Nervous System." MAGENDIE'S original experiment is detailed in the Jour. de Physiol. Expériment., 1822; the mode of demonstrating the facts is described by MICHAEL FOSTER in Handbook for Physiological Laboratory, p. 408.

B.—FUNCTIONS OF THE CRANIAL NERVES.

These are so named from their passing through foramina in the base of the cranium. They are arranged according to different systems, as follows:—

Willis.[1]		Physiological Name.	Soemmering.
First pair,		Olfactory,	First pair.
Second ,,		Optic,	Second ,,
Third ,,		Oculo-motor,	Third ,,
Fourth ,,		Pathetic,	Fourth ,,
Fifth ,,		Trifacial,	Fifth ,,
Sixth ,,		Abducent-ocular,	Sixth ,,
Seventh ,,	*portio dura*	Facial-motor,	Seventh ,,
	portio mollis	Auditory,	Eighth ,,
Eighth ,,		Glosso-pharyngeal,	Ninth ,,
		Pneumogastric or vagus,	Tenth ,,
		Spinal-accessory,	Eleventh ,,
Ninth ,,		Hypoglossal,	Twelfth ,,

Of these, three are exclusively connected with special sensation, namely, the olfactory, optic, and auditory. Two are nerves of common, and partly also of special, sensation, and are combined with motor fibres close to their origin, namely, the fifth and eighth; the fifth having a motor root of its own, and the eighth receiving motor fibres from the spinal-accessory and from the roots of the pneumogastrics. The remaining nerves are all nearly exclusively motor, but some, more especially the facial, are combined with sensory fibres in the course of their distribution.

1. The Olfactory Nerve.

This is the nerve of smell. After its destruction the animal cannot perceive odours, but it is still sensible to irritating vapours such as ammonia.

---

[1] In stating the number of a nerve, Willis' classification will be used.

2. THE OPTIC NERVE.

This is the nerve of vision. Section is followed by blindness. Irritations of any kind excite luminous sensations. The fibres are insensible to the direct action of light, and only respond normally to impressions received from the retina.

3. THE OCULO-MOTOR NERVE.

The oculo-motor, or third, is purely a motor nerve, supplying filaments to all the muscles of the eye-ball with the exception of the external rectus and superior oblique. It also supplies the circular fibres of the iris, and the ciliary muscle. Division of the whole of this nerve at its root causes complete paralysis of the muscles supplied by it; the upper eyelid hangs down and cannot be raised, in consequence of paralysis of the levator palpabræ superioris, and the eyeball is drawn downwards and outwards by the action of the external rectus and superior oblique. There is also dilatation and immobility of the pupil. Stimulation of the distal end of the nerve causes violent convulsive movements of the eyeball and contraction of the pupil. In cases of disease in man paralysing this nerve, the power of accommodating the eye to different distances has been lost or much impaired. The mechanism by which accommodation is accomplished will be described in treating of vision. When the two nerves are intact, the optic axes unite at a proper angle so as to secure simple binocular vision; consequently, paralysis causes divergence of the optic axis on the diseased side, and there is a sensation of double vision, the image on the affected side being apparently somewhat higher than on the other, and crossing it.

4. THE PATHETIC NERVE.

This nerve supplies the superior oblique, and it determines the rotation of the eye, by which the pupil is carried upwards. After division, the pupil is directed somewhat downward and to the side, by the action of the inferior oblique. In these circumstances, there is double vision, but the two images are separate and distinct.

5. THE FIFTH OR TRIFACIAL NERVE.

This nerve consists, at its origin from the side of the Pons Varolii, of two portions of very unequal size, the smaller being the motor portion, whilst the larger, having on it the Gasserian ganglion, is sensory. The lesser or motor root unites with one of the three large branches given off by the posterior root, so that of the three main divisions which separate from each other beyond the ganglion, the ophthalmic and superior maxillary division are purely sensory, whilst the inferior maxillary part is senso-motor. Irritation of the larger root causes pain without any muscular movements, whilst irritation of the smaller root excites convulsive motions of the muscles of mastication without pain. Section of the larger root causes the loss of common sensation in the cutaneous and mucous surfaces of the head and face, in the salivary and lachrymal glands and teeth, loss of taste as well as loss of tactile sensibility on the tip of the tongue. After section, also, it has been observed that from loss of sensibility, the animal has difficulty in mastication.

a. *The Ophthalmic Division.*—This branch is purely sensory. It also exerts an influence over the secretion of tears. Excitation of the lachrymal nerve or of the ophthalmic division causes copious secretion by the gland. Magendie pointed out that after section, the cornea becomes opaque, and keratitis is set up which may result in ulceration and perforation of the cornea. At the same time there is a diminution in the tension of the eyeball. Some have supposed from these results that certain filaments may exercise a nutritive or trophic influence over the tissues of the eye.

b. *The Superior Maxillary Division* is sensory; but it furnishes filaments to the nasal and palatine glands. When cut, the mucus in the nostrils becomes thick and sanguinous, and ulcerative changes may occur in the membrane. The sense of smell is quickly lost, as this nerve supplies vaso-motor filaments to the vessels of the nostril: and also filaments to the nasal glands.

c. *The Inferior Maxillary Branch* is partly sensory and partly motor. One of its most important branches is the lingual which confers both tactile sensibility and the special sense of taste on the anterior portion of the tongue. Section of this nerve abolishes taste, more especially for sweets. Some hold the opinion that the gustative fibres are derived from the chorda tympani, but experimental evidence is very contradictory on this point.

Section of the auriculo-temporal nerve arrests secretion by the parotid gland, whilst irritation of the distal end causes increased secretion. Bernard has shown, however, that such secretory filaments do not belong to the fifth nerve, but come from the facial by the small superficial petrosal nerve. As seen in p. 488, the secretions of the submaxillary and sublingual glands are influenced by the chorda.

The fifth nerve also contains the vaso-motor filaments which accompany the vessels in the oral cavity. Such filaments, aided by the action of such as directly supply mucous glands, no doubt assist in maintaining the nutrition of the structures.

The fibres of the small root of the 5th, as already pointed out, pass entirely to the sub-maxillary division, and they innervate the temporal, masseter, two pterygoids, the anterior belly of the digastric, the mylo-hyoid, and circumflexus palati. A filament passes also from the otic ganglion to the tensor tympani muscle.

Section of the nerve on one side causes the jaw to be pulled to the sound side so that the superior and inferior teeth do not correspond. In the rabbit, where the growth of the incisors is continuous, these teeth may continue to grow, and by attrition side to side become sharp and angular.

d. *The Ganglia in connection with the Fifth.*—These are the ophthalmic, the spheno-palatine or Meckel's, the otic, and the submaxillary. (*a*) *The Ophthalmic.*—Destruction causes insensibility of the cornea. Section of the ciliary nerves which proceed from it is followed by dilatation of the pupil. The motor fibres which supply the circular fibres of the iris come from the third; the sympathetic also supplies motor branches which act on the radiating fibres of the iris; whilst the fifth furnishes all the sensory fibres. The filaments governing the ciliary muscle, in connection with accommodation, come from the third. (*b*) *The Spheno-palatine*, in connection with the superior maxillary division, is so deeply seated as to render experimental results very doubtful. Extirpation does not cause pain, nor is it followed by any alteration in nutrition, nor by modifications in the vascularity of the nasal mucous membrane; smell and taste are also unaffected. The motor fibres of the ganglion are derived from the facial by the great superficial petrosal and the vidian; the sensory filaments come from the fifth; and it also contains sympathetic fibres received from the carotid plexus. (*c*) The *Otic* ganglion, connected with the inferior maxillary, has not been examined experimentally with any degree of success, and our knowledge of the functions of its different roots and branches is derived from anatomical evidence. Some doubt has arisen as to the origin of its motor root: according to Hyrtl, the motor fibres come from a branch of the inferior maxillary supplying the internal pterygoid muscle; whilst Longet has stated that they are filaments of the facial passing through the small superficial petrosal nerve. The sensory fibres are derived from the glosso-pharyngeal by Jacobson's nerve; and the sympathetic filaments come from the plexus surrounding the middle meningeal artery. It has been clearly ascertained that the secretory fibres supplied to the parotid gland come from this ganglion, having reached it from the facial through the small superficial petrosal nerve. (*d*) The facts known regarding the submaxillary ganglion, which, from its readiness of access, has been examined experimentally, are stated at p. 234. The various ganglia just described may be regarded as local reflex centres, associated with local and limited movements or with secretion.

6. THE SIXTH NERVE.

This nerve supplies the external rectus muscle. Section causes the eye to be pulled somewhat inwards; and irritation of the distal end is followed by deviation of the eye to the side.

7. THE FACIAL NERVE.

The seventh pair consists of two nerves, the auditory, connected with the sense of hearing, and the facial. The function of the facial is motor. Section of the nerve at its root is followed immediately by paralysis of the muscles of the face; the countenance is devoid of expression on the affected side; the features are dragged towards the sound side; the mouth is oblique. The affected half of the face is a little more prominent than the sound half, which is wrinkled and contracted. The paralysed side is broader than the sound side, the eyelids are wide open, and the eye appears larger than its fellow. The muscles moving the jaws are still obedient to volition; mastication is easily performed, and substances can be held between the teeth. The lips on one side are paralysed, food collects between the gum and the cheek, and sometimes escapes from the mouth. The pronunciation of labials such as *b* and *p*, and of *o*, is imperfect. With all these symptoms, however, there is no loss of sensibility.

The nerve is therefore to be regarded as the special nerve of expression. It has been difficult to determine with accuracy to what extent sensory filaments may be mixed with the nerve during its passage from its origin through the aqueduct of Fallopius. At its root, there is a small filament connecting it with the auditory; when the nerve enters the aqueduct of Fallopius, it swells into the geniculate ganglion, where it is connected with the spheno-palatine ganglion by the great superficial petrosal nerve, and with the otic ganglion by the small superficial petrosal nerve; and lastly, it receives filaments from the pneumogastric by the auricular branch of that nerve, joining the posterior auricular branch of the facial. Experiment has shown that the facial is insensible at its origin, but that it is slightly sensitive after its issue from the stylo-mastoid foramen. Its sensitiveness in this region, however, has been acquired by anastomosis with other nerves. Claude Bernard showed that after section of the nerve below its anastomosis with the pneumogastric, both cut ends were sensitive; on dividing the pneumogastric branch, sensitiveness disappeared from the central portion. Whilst within the aqueduct of Fallopius, it also gives off a small motor twig to the stapedius muscle, and an important branch, the chorda tympani. The latter is a complex nerve, containing at least three kinds of filaments—some connected with the sense of taste in the anterior part of the tongue; others governing secretion in the salivary glands; and a third distributed to the vessels of the glands. Facial paralysis, caused by disease of the nerve, has also been attended by loss of taste in the tip of the tongue. The influence of the chorda tympani on secretion has often been alluded to. The parotid fibres separate from the facial at the geniculate ganglion, pass through the small superficial petrosal, reach the otic ganglion, from thence to anastomose with the auriculo-temporal branch of the fifth, ultimately terminating in the gland. The submaxillary and sublingual fibres travel through the chorda tympani to the submaxillary ganglion, and thence to the glands. The functions of the nervous band between the facial and auditory are unknown; but Bernard, from various experiments, inclines to the opinion that it is composed of sympathetic filaments, which are ultimately distributed to mucous surfaces and glands.

8. THE GLOSSO-PHARYNGEAL NERVE.

The eighth pair of nerves consists of the glosso-pharyngeal, pneumogastric, and spinal accessory nerves. It is necessary to consider them separately.

The glosso-pharyngeal is sensory at its origin. It contains also numerous filaments, distributed to the back of the tongue and the fauces, which act as sensory fibres in the reflex mechanisms of deglutition and vomiting. It also confers the special sense of taste to the posterior third of the tongue. Its section diminishes gustatory sensibility over the whole of the tongue, especially for bitter substances. It is not, however, the only nerve of taste, as the chorda tympani and lingual branch of the fifth, also contain gustatory fibres. It probably also contains motor fibres for the stylo-pharyngeal and middle constrictor muscles, and a few vaso-motor fibres.

9. The Pneumogastric or Vagus Nerve.

The pneumo-gastric nerve arises from the medulla oblongata, in a line below the last nerve; and the deep fibres may be traced into the grey matter near the floor of the fourth ventricle. Two ganglia are situated on its roots; the upper one, small and rounded, in the foramen lacerum; the lower, elongated and plexiform, at the place of origin of the superior laryngeal branch of the nerve. Nearly all the fibres of the roots of the nerve pass through one or other of these ganglia; a few of those arising lowest down from the medulla appearing to pass the ganglia without being involved in them. Besides these fibres, the pneumo-gastric nerve is joined, between the ganglia, by the internal portion of the spinal accessory nerve, constituting a considerable bundle of fibres which may be traced past the lower ganglion, and which contributes mainly to form the motor part of the vagus. The vagus is connected near its root with the sympathetic, glosso-pharyngeal, hypoglossal, and some of the upper spinal nerves. The functions of the pneumo-gastric have already been partially described in relation to the nervous arrangement of the heart, lungs, stomach, and liver; but a brief *resumé* will now be given:—

a. Irritation of the root causes pain, but there is much more pain if the stimulus be applied to the trunk of the nerve below the place where the superior laryngeal branch is given off. It is evident, therefore, that the pneumo-gastric contains ordinary sensory nerves which originate in the mucous membrane of the air passages, the base of the tongue, palate, pharynx, œsophagus, and stomach. Such fibres may also originate in the heart and bile ducts. From many of these situations, they probably transmit impressions which result in such sensations as hunger, thirst, a feeling of repletion, or those referable to the respiratory organs.

b. Irritation of the superior laryngeal branch causes pain and contraction of the crico-thyroid muscle; section paralyses the muscle, causes hoarseness, and destroys the sensibility of the larynx. Irritation of the inferior or recurrent laryngeal causes no pain, but excites contraction in all the muscles of the larynx, with the exception of the crico-thyroid; section causes paralysis of the muscles of the larynx, abolishes voice, and there is a risk of suffocation. The superior laryngeal is therefore evidently, with the exception of its twig to the crico-thyroid, and, according to some, a branch supplying half the arytenoid, a sensory and afferent nerve; whilst the inferior laryngeal is the principal motor and efferent nerve, along which impulses pass to the laryngeal muscles, causing the necessary movements in voice.

c. In addition to the *motor* fibres passing to the larynx, the vagus supplies motor filaments to the following muscles: the azygos uvulae, the palato-glossus and palato-pharyngeus, the constrictors of the pharynx, and the muscular coats of the œsophagus and stomach; probably also to the fibres found in the bronchia of the lungs. Various observers have seen movements of other organs on stimulating the distal end of the divided nerve. For example, such movements have been seen in the spleen, uterus, and bladder; but from the difficulty of cutting off all other nervous communications, these results are very doubtful.

d. It has already been shown (p. 329) that the vagus contains at least two sets of fibres related to the heart:

(1) *inhibitory*, the function of which is to restrain the activity of intra-cardiac ganglia, and (2) those of the *depressor nerve*, which act upon the vaso-motor centre in the medulla. Possibly, also, it may contain fibres conveying ordinary sensory impressions to the brain, an increased excitability of which may give rise to such feelings of distress and agony as are experienced in angina pectoris.

e. Four sets of fibres are also probably distributed to the stomach: motor, influencing its movements; sensory, conveying impressions of ordinary sensibility or of pain; inhibitory, as pointed out by Rutherford, which restrain the activity of the vaso-motor centre in the medulla, acting through the splanchnic nerves; and secretory, influencing the formation of gastric juice. The latter influence is doubtful, as experiments have been indecisive.

f. Experiments have also shown, as already described on p. 404, that the vagus, as related to the process of respiration, contains four sets of fibres: (1) ordinary sensory fibres; (2) pulmonary fibres, the activity of which excites the inspiratory and paralyses the expiratory centre; (3) laryngeal fibres, which so act as to excite the expiratory and paralyse the inspiratory centre; and (4) motor fibres distributed to the walls of the bronchia.

g. Bernard has stated that irritation of the pneumogastric increases the quantity of sugar and glycogen in the liver. Section of the nerve below the heart and lungs is not followed by any effect on the glycogenic function, whilst irritation of the central end is followed by the appearance of sugar in the urine. As already stated in p. 431, these facts indicate that the influence of the vagus on the formation of glycogen is only indirect, and is explained by the effect of some of its filaments on the vaso-motor centre.

10. The Spinal Accessory.

This nerve is exclusively motor. Its external branch, derived from the cord, supplies the sterno-cleido-mastoid, along with branches of the cervical plexus; its internal branch, springing from the medulla, gives motor fibres to the vagus which supply the muscles of the larynx through the recurrent laryngeal. Experiments by Bernard also show that, in phonation, this nerve acts, by its internal branch, chiefly upon the glottis, the organ producing sound by the vibration of the vocal cords in a state of tension; whilst through its external branch, by regulating the action of the sterno-mastoid and trapezius, it controls the amount of air expelled during the emission of sound. He found that, after section of the external branch, there was shortness of expiration and great breathlessness, especially when the animal moved quickly, owing to the want of a regulated discharge of air being sent through the glottis. Irritation of the central end of the divided spinal-accessory nerve causes pain, probably on account of its anastomosis with the vagus and with the posterior roots of spinal nerves.

11. The Hypoglossal or Ninth Nerve.

This nerve is distributed entirely to muscles: these are the hyo-glossus, stylo-glossus, genio-glossus, and lingualis; and by its descending branch, along with the parts of the third and fourth cervical nerves with which it is united, to the thyro-hyoid, sterno-hyoid, sterno-thyroid, and omo-hyoid muscles. At its root, it is entirely motor. Irritation of the root does not cause pain; but when applied to the branches of the nerve it may do so, probably owing to anastomoses with sensory nerves. Section paralyses the muscles of the tongue, and renders articulation in speech, and the first act of deglutition, difficult.

Here it may be pointed out that the innervation of the tongue is as follows: *motor* filaments are derived entirely from the hypoglossal; *sensory* filaments of two kinds, namely (1) sense of touch, chiefly due to the lingual branch of the fifth; and (2) sense of taste to (*a*) glosso-pharyngeal, for the posterior third, and (*b*) chorda tympani and lingual of the fifth, for the anterior two-thirds. The vessels of the tongue obtain vaso-motor branches from the sympathetic.

Consult (*1st pair*) CLAUDE BERNARD, Leçons sur la Phys. et la Path. du Système Nerveux, p. 226; (*3rd pair*) FRANCES, Essais sur la Paralysie de la 3° Paire, 1854; (*4th pair*) SZOKALSKY, De l'Influence des Muscles Obliques sur la Vision, 1840; (*5th pair*) CHARLES BELL, In collected writings on Nervous System; MAYO, In Anatomical and Physiological commentaries; MAGENDIE, Journal de Physiologie, 1822, 1824; LONGET, Anat. and Physiol., der System Nerv.; (*6th pair*), BERNARD ET LONGET, ut supra; (*7th pair*) Treatises by BELL, MAYO, MAGENDIE, and LONGET, above noted; VULPIAN, Recherches sur la Corde Tympane, 1873; (*8th pair*), JOHN REID'S Works, 1844; SPENCE, in Edin. Med. and Surg. Journal, 1842; BROWN-SÉQUARD, Gazette Medical, 1854. An elaborate account of the physiology of the cranial nerves will be found in FLINT'S Physiology, and in BEAUNIS' Physiologie.

C.—FUNCTIONS OF THE SYMPATHETIC NERVE.

1. GENERAL ANATOMICAL ARRANGEMENTS.

The fibres of the sympathetic system found in any part of the body consist of two kinds: (1) of grey or gelatinous fibres, destitute of the white substance of Schwann (Fig. 121, *g*); and (2) of medullated fibres similar to those met with in the cerebro-spinal nerves. The grey fibres originate chiefly in the ganglia so prevalent in the sympathetic system, whilst the tubular fibres are derived from the cerebro-spinal system. The trunk of the great sympathetic nerve constitutes a chain of swellings, connected by intermediate cords of grey nerve fibres, and extending nearly symmetrically on each side of the vertebral column, from the base of the cranium to the coccyx. On this part of the nerve, 24 or 25 ganglia are placed on each side. This great trunk, as it passes along the spine, is connected with the spinal nerves, the connecting fibres being of two kinds, one consisting of white or tubular, and the other of grey or gelatinous fibres. The first set of these connecting cords conveys cerebro-spinal fibres into the sympathetic system, and the second transmits grey fibres from the sympathetic into the cerebro-spinal nerves. Allen Thomson has remarked that "in the frog, the white communicating twigs between the spinal and sympathetic nerves prevail at the upper part of the spine, becoming smaller, or ceasing altogether at the lower part, whilst the grey communicating twigs remain there of their full size." (Physiology, p. 155.) The general conclusion is that, while the grey fibres predominate in the sympathetic nerves, and the medullated in the cerebro-spinal, these two elements are mixed in various proportions in both of the great divisions of the nervous system.

At their lower extremities, the main trunks of opposite sides generally unite in the middle line; and at the upper ends, each trunk, after being connected with the eighth and ninth cranial nerves external to the cranium, passes into that cavity along with the internal carotid artery, and there, as well as in other situations, comes into connection with all the remaining cranial nerves, except the olfactory, auditory, and optic. This conjunction may be effected directly, as with the fourth, sixth, and ninth nerves; or through a ganglion, as the ophthalmic, with the third and fifth; the spheno-palatine, otic, and submaxillary, with the fifth and facial: the geniculate, with the facial; the jugular, with the glosso-pharyngeal; and with the vagus, through one of its own ganglia. On the fibres of the sympathetic distributed to the viscera, numerous ganglia, or plexuses in which ganglia exist, are met with, and frequently there is a plexus following the course of each great vessel. Thus, we find the sympathetic contributing to the innervation of all the glands and viscera in each region of the body, and the details are recorded in any anatomical work.

2. THE RESULTS OF EXPERIMENT.

Certain of the results obtained by cutting or irritating the sympathetic nerve have already been stated in describing the innervation of the heart, stomach, &c. It has been shown that if the sympathetic be cut in the neck, there is a dilatation of the vessels, both superficial and deep, on the affected side, an increased supply of blood, elevation of temperature, contraction of the pupil, and an increase of all the secretions, as shown by sweating and the secretion of tears. These results were partially revealed by Petit in 1727, by Dupuy in 1816, by Brachet in 1837, and by John Reid in 1838; but it was not until 1852 that their full significance was shown, their cause specifically stated, and the special discovery of the increase of temperature was made, by Claude Bernard. Soon afterwards, Brown-Séquard demonstrated that irritation of the cephalic end of the divided nerve was followed by the gradual disappearance of all of these effects, thus completing the experimental demonstration of the influence of the sympathetic on vessels. These investigations led to the recognition of the sympathetic as the nerve supplying the contractile coats of vessels with nervous energy, so as to keep them in a state of partial contraction. Cut the nerve, and the vessels will dilate; stimulate the end next the vessels, and they will contract. Such nerves have received the name of *vaso-motor*, or constrictor nerves of the vessel. The next question to be determined was as to their origin. Anatomists, as already pointed out, had shown that numerous connections existed between the cerebro-spinal and sympathetic systems, and physiologists, by severing these connections and by cutting portions of the cord or medulla, endeavoured to discover the effects thereby produced. The following are the general results arrived at:—

a. The vaso-motor fibres of the head are supplied by the cervical portion of the sympathetic, and originate in the cervical region of the cord, proceeding from it by the anterior roots of the lower cervical and upper dorsal nerves. The motor fibres supplying the radiating fibres of the iris also originate in the same region, so that section of the sympathetic in the neck paralyses these fibres, the result being contraction of the pupil, from the influence of the third nerve, supplying the circular fibres being unopposed.

b. The vaso-motors of the upper limbs and of the thorax come—(1) from the inferior cervical and superior thoracic ganglia, and (2) from the cord, by communicating branches between the third and seventh dorsal vertebrae.

c. The vaso-motors of the lower limbs come from the cord through the sciatic and crural nerves; whilst those of the pelvic organs are derived from the abdominal ganglia of the sympathetic.

d. The vaso-motors of the abdominal viscera exist chiefly in the splanchnic nerves; but some fibres supplying the stomach appear to be derived from the pneumogastric.

a. *The Functions of the Splanchnic Nerves.*

These nerves, three in number—"the greater, the lesser, and the smallest"—all arise in man from the thoracic ganglia of the sympathetic, from the fifth to the tenth (greater), tenth and eleventh (lesser), and twelfth (smallest) thoracic ganglia of the sympathetic. The first two appear to supply chiefly the stomach, liver, spleen, pancreas, and intestines; whilst the second and the third disappear in the plexus passing to the kidneys. It must be admitted that the ultimate distribution of each, at least so far as man is concerned, is imperfectly known. When exposed and divided in the lower animals, the abdominal viscera become engorged with blood—there is consequently greatly diminished blood pressure in other portions of the circulation, as may be shown by connecting a kymograph with the carotid artery; irritation of the distal end causes contraction of vessels and an elevation of blood pressure generally. These facts show that, whatever other functions they may have, the splanchnics are the great vaso-motor nerves of the abdominal viscera; but it is likely they also contain fibres which may directly influence secretion. Some have stated that irritation of the nerves inhibits or restrains intestinal movements.

b. *The Vaso-motor Fibres of the Extremities.*

These are contained in the nervous trunks familiar to anatomists. Section of the sciatic nerve causes dilatation of the vessels of the affected limb, and usually swelling. This may be readily demonstrated in the frog by having the web of the foot under the microscope and observing the effects of section. A similar effect has been seen in the limbs of man during paralysis from the influence of extreme cold.

c. *Relation of the Vaso-motor Filaments to the Cerebro-spinal System.*

In 1832, Nasse showed that there was an elevation of temperature in the limbs after section of the spinal cord; and in 1852, Brown-Séquard discovered that section of one half of the cord, in the dorsal region, was followed by an increase of temperature in the opposite posterior extremity. The rise in temperature was found to be coincident with an increase in the calibre of the vessels. On stimulating the distal end of the cord, Pflüger found that the vessels contracted and the temperature fell. These facts indicate that at least a portion of vaso-motor filaments come from the cord, and the next point to be ascertained is, do they come from several segments, or from one more than another? Here there are great differences of opinion among observers. Some think that vaso-motor centres are scattered throughout the cord; whilst others are of opinion that the chief centre at all events is in the medulla oblongata, as stated at p. 367. The latter view is supported by the experiments of Ludwig and Owsjannikow, which clearly show that when a particular part of the medulla oblongata is severed, there is at once a dilatation of the smaller vessels throughout the body, and a consequent fall of pressure in the larger vessels. The following *resumé* shows at a glance the general functions of the sympathetic, as at present determined by experiment:—

I. The *Cervical Sympathetic* contains—

1. Vaso-motor fibres for the same side of the head.
2. Accelerating fibres for the heart (p. 332).
3. Fibres which supply the dilating fibres of the iris.
4. Fibres for the salivary and lachrymal glands.
5. Afferent fibres which excite the origin of the inhibitory fibres of the vagus (p. 332).
6. Afferent fibres which may stimulate the vaso-motor centres.

II. The *Thoracic Sympathetic* contains, either in filaments proceeding from its ganglia, or in the splanchnic nerves—

1. Vaso-motor fibres for the vessels of the abdominal viscera.
2. Inhibitory fibres, restraining the movements of the intestinal wall.

3. Fibres, the section of which is followed by appearance of sugar in the urine.

III. The *Abdominal* and *Pelvic Sympathetic* probably contain fibres supplying the vessels of the parts, but we have no exact information on the subject.

d. *General Illustrations of the Influence of the Sympathetic.*

Though much of the exact mechanism is still obscure, it is important to notice the influence which the sympathetic exerts on the processes of nutrition and of excretion. It probably exerts this influence chiefly through the filaments by which it governs the calibre of vessels; thus regulating the supply of blood to a part, and promoting or diminishing, as the case may be, the interchanges constantly taking place between the blood and the tissues. Some have supposed that such filaments may exert a directly nutritive effect, becoming what they have called *trophic*, or nutritional; but such an influence cannot be explained by any theory of nervous activity at present held, nor by any histological observations. So far as observation goes at present, the filaments of the sympathetic are distributed only to the involuntary fibres of organs, such as those of the iris or of the stomach, or of vessels, in both instances, causing movements of a slow and possibly of a rhythmic character. All the phenomena of the sympathetic may be accounted for on this basis, without supposing that they exercise any direct influence either on secreting structures or on the growth and development of tissue. The question of whether or not there are *afferent* fibres in the sympathetic, conveying impressions which may excite reflex actions of one kind or another, is not settled. Direct experimental evidence is in favour of the view that there is no action of this kind, and that the majority of fibres in the sympathetic system convey impulses centrifugally, affecting the vessels of glands, of membranes, or of tissues generally. Still, it must be confessed that we know nothing whatever, either by inference from histological observations, or by direct experiment, of the actions of the so-called non-medullated or grey fibres; and it is possible they may have some kind of direct effect at present unknown. The importance of renewed investigations in this field of enquiry can scarcely be overrated. Many of the phenomena of fever, cholera, acute rheumatism, inflammation, &c., have been accounted for by affections of the sympathetic; but the kind of information offered is hypothetical and unsatisfactory.

D.—FUNCTIONS OF THE NERVES OF SPECIAL SENSE.

The various kinds of sensory impressions are (1) the sense of touch; (2) the sense of taste; (3) the sense of smell; (4) the sense of vision; and (5) the sense of hearing. All of these are produced by a process which may be conveniently divided into three portions: (1) the action of some kind of external stimulus on a terminal organ, connected with the fibres forming the nerve of special sense; (2) transmission along the nerve of some kind of activity corresponding to the external stimulus; and (3) the reception of the impression in some portion of the brain, the result being a consciousness of the impression, or, as it is generally termed, a sensation. Thus, in the case of vision, the specific stimulus is light, the terminal organ is the retina, the transmitting fibres are in the optic nerve, and the recipient apparatus is in the brain. Light has no influence on the brain itself, nor on the nerve, but only on the retina. The normal stimulus to the nerve is some kind of irritation proceeding from the retina, but it is important to note that while both the retina and the nerve may be stimulated by other activities than light, such as mechanical pressure, electricity, or heat, the sensational result is always of a luminous character. Thus, a blow on the eye, pressure on the eyeball, intermittent pressure on the nerve, electric shocks sent to the posterior part of the eyeball, or severance of the optic nerve, always produce luminous impressions which vary in intensity and character according to the nature and strength of the stimulus. The same is true of all the other senses. It is evident, therefore, that the impressions transmitted along each nerve of special sense to the brain may set up various kinds of activity in that structure. A description, however, of the organs of sense involves so many details not strictly related to their nervous mechanism, but connected with purely physical conditions, as to make it inexpedient to enter upon it at this stage. Further, the student will be better able to comprehend the physiology of the senses after he has acquired some information regarding the functions of the great centres.

II.—FUNCTIONS OF THE GREAT CENTRES.

The nerve centres consist of (1) the spinal cord; (2) medulla oblongata; and (3) the encephalon. The latter is chiefly formed by the cerebral hemispheres, corpora striata, optic thalami, corpora quadrigemina, and cerebellum.

A.—GENERAL ANATOMICAL CONDITIONS.

1. General View of the Nervous System of Invertebrates.

In none of the *Protozoa*, including such animals as sponges, infusoria, &c., has any trace of a nervous system been discovered. Neither is any rudiment of it to be found in the *Hydrozoa*,[1] the first subdivision of the cœlenterate group of animals; but in *Actinozoa*, which comprehends such animals as the sea-anemone, it is first discovered as a little knot or nodule of nervous matter, from which delicate fibres radiate. Such a nodule is called a *ganglion*, and the filaments constitute *nerves*. Among the *Echinodermata*, such as star-fishes, sea-urchins, &c., we find the nervous system consisting of a number of ganglia, connected together, so as to form a ring or *nervous circle*, from which nerve filaments pass to various parts of the body. In some of the *Annelidæ*, or worms, we find (Fig. 123, A), a ganglion, *a*, in the neighbourhood of the head, from which two nervous cords pass along the ventral surface of the animal. In the *Mollusca* there are usually at least three ganglia with radiating nerves—one in the head, one in the foot, and one posterior and above the alimentary canal. In the *Insecta* (Fig. 123, C), we find a large ganglion, *a*, in the head, from which a double cord passes backwards along the *ventral* surface of the animal, and in connection with which there are three or more ganglia, as seen in the figure. In the *Crustaceæ*, such as

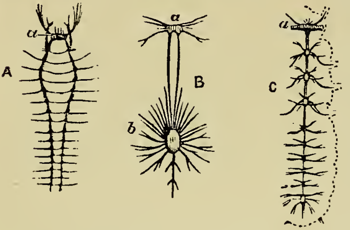


FIG. 123.—Typical forms of nervous system in invertebrates. A, nervous system of a *Serpula*, a marine annelide: *a*, cephalic ganglion. C, nervous system of an ant: *a*, cephalic ganglion. B, nervous system of a crab: *a*, cephalic ganglion; *b*, mass of ventral ganglia fused together.

---

[1] G. J. Romanes has recently pointed out, in a series of remarkable researches on Medusæ, that in these animals we find phenomena similar to nervous transmission sent along definite tracks, or sometimes diffused from one part of the body to the other, without any histological trace of differentiated nerve fibre. We have here an example of the early stages of the evolution of a nervous system.

the common crab (Fig. 123, B), there is a large ganglion near the anterior extremity, with nerves for the eyes and antennæ, *a*, while behind we find the ventral chain of ganglia fused into one mass, *b*.

2. General View of the Nervous System of Vertebrates.

All of the groups now mentioned belong to the invertebrate subdivision of the animal kingdom, and all have their nervous system along the *ventral* surface of their body. In vertebrates we find the principal portion of the nervous centres forming an elongated mass along the *dorsal* aspect of the animal, constituting the *cerebro-spinal axis*. This consists, as illustrated by diagram (Fig. 124), of a chain of ganglia constituting the *brain*, behind which there is an elongated mass of nervous matter running from the brain through the canal of the vertebral column, and called the *spinal cord*. In all vertebrates, the cord seems to be much alike in general structure and arrangements, but one animal differs from another (as a fish from a frog, or a pigeon from a rabbit) by the degree of development of the brain. This consists of a series of ganglia, which, in a typical or ideal

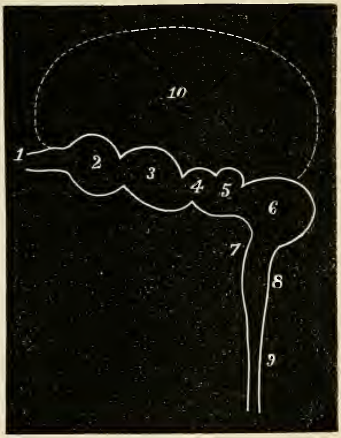


Fig. 124.—Diagram of an ideal or typical brain. 1, olfactory lobes; 2, cerebrum; 3, corpus striatum; 4, optic thalamus; 5, optic lobe; 6, cerebellum; 7, pons Varolii; 8, medulla oblongata; 9, spinal cord. The dotted curve indicates the possible development of the cerebral lobes.

brain, might be thus represented, Fig. 124: (1) olfactory lobes; (2) cerebral lobes; (3) corpora striata; (4) optic thalami; (5) optic lobes; (6) cerebellum; (7) pons Varolii; and (8) medulla oblongata. Such a brain, for example, is seen in many *fishes* (Fig. 125), where the cerebral hemispheres, 2—, are still of very small size. The same arrangement may also be seen in the brain of *Amphibians*, such as the common frog (Fig. 126); but here we find the cerebral lobes larger, so that they now extend backwards, and cover the *corpora striata*. When we ascend to reptiles, such as the tortoise (Fig. 127), we find the cerebral hemispheres larger, broader, and thicker as regards the amount of grey matter on the surface. In the interior of the hemispheres, also, we find the first appearance of cavities termed *ventricles.* The hemispheres are also partially united by a band of fibres, called the *corpus callosum.* The cerebellum (4) is still feebly developed. In birds, the cerebral hemispheres have undergone a considerably greater

FIG. 125.—Brain of common Gurnard. 1, olfactory; 2, cerebral lobes; 3, corpora striata; 4, cerebellum.

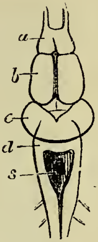


FIG. 126.—Brain of common Frog. *a*, olfactory; *b*, cerebral lobes covering corpora striata; *c*, corpora quadrigemina, or optic lobes; *d*, cerebellum (rudimentary); *s*, back of medulla, showing fossa.

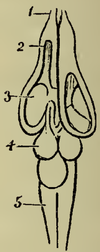


FIG. 127.—Brain of Tortoise. 1, olfactory; 2, cerebral lobes; 3, corpora striata; 4, optic lobes; 5, cerebellum; 6, medulla. Part of the surface of the cerebral lobes has been removed to show the cavities in the interior, termed the *ventricles.*

enlargement, as seen in Fig. 128. The cerebellum, that is, its medium lobe, which alone is yet visible, has become much larger, and is divided into transverse laminæ; an imperfectly-formed swelling at the upper part of the medulla, called the *pons Varolii*, is now seen; and the *corpus callosum* extends farther backwards, and is more developed than in reptiles. In the lower orders of Mammalia, as Marsupialia and Edentata, the corpus callosum and fornix are still imperfect, as in birds, and the cerebellum still exists chiefly in its median portion. A small pons Varolii has now, however, made its appearance, and is visible superficially, constituting a commissure for the cerebellum, along with the lateral parts of which it is developed.

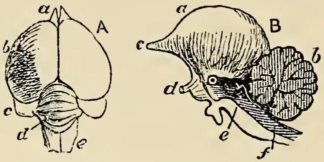


FIG. 128.—Brain of Pigeon. A, view from above; B, lateral view of a bisected brain. A—*a*, olfactory; *b*, cerebral lobes; *c*, optic lobes; *d*, cerebellum; *e*, medulla. B—*a*, cerebrum; *b*, cerebellum; *c*, olfactory; *d*, optic nerves; *e*, medulla; *f*, cord.

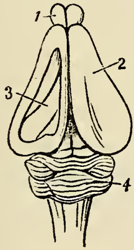


FIG. 129.—Rabbit's Brain. 1, olfactory; 2, surface of cerebral hemisphere; 3, cavity in brain, called a *ventricle*, in the floor of which is seen the *corpus striatum*; 4, the cerebellum.

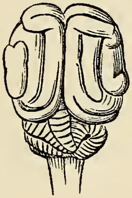


FIG. 130.—Cat's Brain, showing convoluted surface. Contrast the form of the cerebellum in the cat and rabbit. In the former the central lobe is small, whilst the lateral are largely developed.

In these orders, and in the Rodentia (Fig. 129), the cerebral hemispheres present scarcely any convolutions; and they are not large enough to cover the cerebellum, nor even, in some, the corpora quadrigemina. In the remaining orders of Mammalia (Fig. 130), the cerebral hemispheres continue to enlarge, chiefly inferiorly and posteriorly; and the convolutions make their appearance, and increase in number and depth. The middle cornua of the lateral ventricles are present; the lateral lobes of the cerebellum become more apparent, but are still inferior in size to the middle one, and along with them the size of the pons increases; the corpus callosum and fornix (a band of longitudinal commissural fibres) are developed from before backwards; the corpora quadrigemina, the same structures as form the optic lobes in birds and reptiles, are proportionately large and in many still hollow; the olfactory lobes are large, and contain a cavity which communicates with the lateral ventricle; whilst the posterior cornua of the lateral ventricle, the posterior lobes of the cerebral hemispheres and *pes hippocampi* are still absent. In the dog, and still more in the elephant, the convolutions are numerous and deep. The Cetacea have a proportionally smaller brain, the surface of which, however, shows many convolutions.

In the greater number of Quadrumina, the brain does not attain a higher degree of development than that of the mammalia in general, as now noticed; but in the chimpanzee, orang, and gorilla, in addition to the increased proportionate size of the whole brain, an approach to the human configuration and structure is very perceptible; as in the development of the posterior lobes of the hemispheres and posterior cornua of the lateral ventricles, the presence of the pes hippocampi; the increased number of the convolutions, and a slight degree of want of symmetry between those of the opposite hemispheres; the separation of the corpora albicantia; the proportional increase of the lateral lobes of the cerebellum and the pons Varolii. The whole brain is about one-fourth the actual size of that of man, and the cerebellum is proportionally large.

The following statement shows, in round numbers, the average proportion of the weight of the brain to that of the body, in different classes of animals; but from this scale there are many individual deviations:— (*Allen Thomson.*)

Fishes, .	1 to 4000 or 6000.	Mammals, .	1 to 180.
Reptiles, .	1 to 1500	Orang, .	1 to 120.
Birds, .	1 to 220	Man, .	1 to 40.

3. Special Anatomical Facts relating to Spinal Cord.[1]

This portion of the cerebro-spinal axis extends, within the vertebral canal, from the atlas to the space between the first and second lumbar vertebræ. The cord and its coverings do not entirely fill the vertebral canal, but are suspended loosely within it, the spaces being filled by bloodvessels, fat, &c., so as to allow of considerable motion of the vertebral column without injury to the cord. The roots of the spinal nerves are contained in the canal, gradually becoming longer as they proceed from its lower part, below which the long roots of the lower nerves are continued as the *cauda equina* in the lumbar and sacral portions of the cord. The cord shows a slight enlargement or swelling at the origin of the axillary, and at the origin of the sacral nerves. These swellings are present in all animals in which the limbs exist, and their size is proportionate to the size of

---

[1] The anatomical arrangements of the various parts of the cerebro-spinal system are fully detailed in any anatomical work (Quain, II., p. 489), and are here alluded to in so far as is necessary for comprehending our present knowledge of their functions.

the respective limbs. The general arrangements of the cord are shown diagrammatically in Fig. 131.

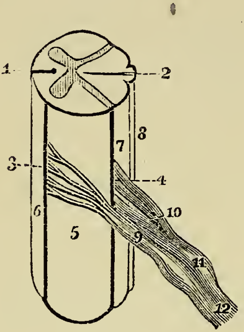


Fig. 131.—Side View of the Spinal Cord, showing the Fissures and Columns: 1, anterior median fissure; 2, posterior median fissure; 3, anterior lateral fissure; 4, posterior lateral fissure; 5, lateral column; 6, anterior column; 7, posterior column; 8, posterior median column; 9, anterior root; 10, posterior root; and 11, ganglion of 12, a spinal nerve. (From Gray's *Human Anatomy*.)

The cord consists externally of white, and internally of grey matter. The white matter, composed as already stated entirely of fibres, forms a series of strands or columns in each half of the cord. Thus, proceeding from the anterior median fissure, we find the anterior column; beyond this, between the roots of the spinal nerves, what is called the lateral column; and between the posterior root and the posterior median fissure, we have the posterior columns. From the absence of any marked line of demarcation between the anterior and lateral columns, each half of the cord, so far as the white matter is concerned, is frequently spoken of as consisting of antero-lateral and posterior columns. These distinctions have also a physiological significance. The grey matter in the centre of the cord is arranged in two crescentic masses, and shows under the microscope numerous multipolar cells, connected with nerve fibres, and imbedded in neuroglia. When traced in numerous thin sections, it has been ascertained that a few of the fibres of an anterior root of a spinal nerve entering on one side of the cord pass over to the other side, at the bottom of the anterior median fissure, and then continue their passage upwards towards the brain; the great majority, however, do not thus decussate but pass up on the same side as high as the medulla oblongata. The posterior roots contain fibres which apparently divide into three sets, the majority, entering the grey matter, disappear, some decussate into the posterior column on the opposite side, whilst the remainder, few in number, pass up upon the same side. These are the general facts shown by histological research.

4. SPECIAL ANATOMICAL FACTS RELATING TO THE MEDULLA OBLONGATA.

The medulla oblongata constitutes the prolongation of the spinal cord upwards, and unites it with the brain. Nearly the same columns of grey and white substance that exist in the cord are to be recognized in the medulla, but are modified by changes in form, structure, and relative position, and combined with several new fasciculi, and masses of grey matter. The greater part of the fasciculi of the medulla may be traced upwards into the brain, some proceeding towards the cerebellum and others to the cerebrum. It is doubtful whether any fibres pass directly to or from the encephalon and the lower portions of the cord; many physiologists are of opinion that direct continuation is at all events not the rule, and that the majority of fibres, both from above and from below, find a new point of departure in the cells of the medulla. Still the tracts along which nervous transmission probably takes place may be traced from below upwards, as follows: (1) the fibres forming the *anterior column* divide into two portions, passing to the same side of the encephalon: (*a*) a small band which ultimately reaches the cerebellum; and (*b*) a portion separated by anatomists into two strands, which reach the corpora quadrigemina and the cerebral hemispheres: (2) the fibres forming the *lateral column* pass partly to the cerebellum on the same side, partly to the cerebrum on the same side, and partly to the cerebrum on the opposite side; and (3) the greater portion of the posterior column passes to the cerebellum, a small part, the *fasciculus gracilis*, going to the cerebrum. It is important to note that each column of the cord, through the medulla, is thus connected both with cerebrum and with cerebellum These general facts may be impressed on the memory by the aid of the following table :—

PRINCIPAL FASCICULI OF THE MEDULLARY FIBRES TRACED FROM SPINAL CORD THROUGH THE MEDULLA OBLONGATA INTO THE BRAIN.

Columns of Spinal Cord.	*Divided into*	*Continued in the Medulla Oblongata, a*	*And pass into the*	
I. ANTERIOR	1. Small division called Band of Solly.	Part of restiform body.	Cerebellum.	....
	2. Portion surrounding olivary nucleus.	Part of olivary fasciculus.	....	Corpora quadrigemina and cerebral hemispheres.
	3. Outer fibres.	Outer part of anterior pyramid.	....	Cerebrum.
II. LATERAL	1. Fibres from surface and deep part.	Part of restiform body.	Cerebellum.	....
	2. Decussating fibres.	Anterior pyramid.	....	Cerebrum.
	3. Remainder.	Fasciculus teres.	....	Cerebrum.
III. POSTERIOR	1. Fasciculus cunietus or all the fibres with the exception of the posterior median column.	Part of restiform body.	Cerebellum.	....
	2. Posterior median column, or fasciculus gracilis.	Posterior pyramid.	....	Cerebrum.

Towards the centre of the medulla, histological research has shown the origins of various nerves. Recollecting that in the spinal cord the anterior roots of the spinal nerves originate chiefly from the anterior part of the grey matter, and the posterior roots from the posterior part, one can readily conceive that in the grey matter of the medulla, which is differentiated, three systems of nerve roots are met with: (1) corresponding to anterior horns of grey matter; (2) to the posterior horns; and (3) intermediate. Thus, to the third class belong the spinal nerves, the pneumogastric, the glosso-pharyngeal, the facial, and the anterior root of the fifth; to the first, the hypoglossal and the motor oculi or third; and to the second, the posterior root of the fifth.

5. Special Anatomical Facts relating to the Encephalon.

The encephalon includes a number of organs more or less distinct from each other, but still connected by numerous bands of fibres. The largest of these organs are the cerebrum and cerebellum. Overlapped by the former, we find, from before backwards, the corpora striata, optic thalami, and corpora quadrigemina, constituting what are frequently termed the *basal ganglia*. In addition, we have at the upper part of the medulla an enlargement termed the pons Varolii. With the view of comprehending the functions of these various parts, it is necessary to point out a few anatomical facts of physiological significance.

a. *The Pons Varolii.*

This consists essentially of fibres passing in two directions, viz., longitudinally, connecting the brain above with the medulla and cord below; and transversely, connecting the lateral hemispheres of the cerebellum, thus forming what is termed the middle peduncle of that organ. Mixed up with these fibres, we find various nuclei, or deposits of grey matter, into which the roots of several of the *cranial* nerves may be traced. Thus, the pons is commissural or connecting in two directions, and at the same time has special deposits of grey matter.

b. *The Cerebellum.*

In connection with the physiology of this organ, it is important to note how it is connected with the rest of the cerebro-spinal axis. It has three peduncles: (1) the *superior peduncles*, crura ad cerebrum, or processus ad testes, together with the valve of Vieussens, a lamina stretched between them, connect the cerebellum with the cerebrum; (2) the *inferior peduncles*, crura ad medullam, are the upper extremities of the restiform bodies; (3) the *middle peduncles*, or crura ad pontem, much the largest, are the lateral extremities of the transverse fibres of the pons Varolii. They connect together the two halves of the cerebellum inferiorly. All these peduncles pass into the interior of the cerebellum at its fore part. (*Quain.*) In the interior of the organ, where the peduncles enter, we find a nucleus of grey matter, called the *corpus dentatum*, and the cortical part is also formed of grey matter, consisting of two distinct layers: an external, which is finely molecular; and an internal, consisting of numerous granular cells. At the junction of these, in a thin section, we find a single layer of large cells, called the *cells of Purkinje*, shaped somewhat like tadpoles, the tails, which are branched, being directed towards the surface of the cerebellum.

c. *Corpora Quadrigemina.*

These bodies, represented in birds, reptiles, and fishes, and in the marsupialia and monotremata, by the optic lobes, are four rounded masses, placed two on each side of the middle line, one pair before the other. The two anterior, the *nates*, are connected with the optic thalamus and with the optic tract; the posterior, the *testes*, are related to the cerebral peduncle. By the superior peduncle of the cerebellum, they are also connected with that organ. It is important, therefore, to observe that they have anatomical connection with the organs of vision, through the optic tracts, with the cerebrum, through the optic thalami, with the cerebellum, and also with the cerebral peduncles. They contain layers of grey matter intermixed with fibres.

d. *Optic Thalami and Corpora Striata.*

Overlapped by the hemispheres of the cerebrum, and deeply imbedded in their white substance, there are two large ganglionic masses, the optic thalami and corpora striata. The latter are anterior to, and placed a little to the outer side of, the former. The thalami receive inferiorly and posteriorly fibres coming from the cerebral peduncles and from the corpora quadrigemina. It is probable that few such fibres pass directly through the thalami; but, as Kölliker supposes, they may be connected with those fibres which radiate from the thalami into the cerebral hemispheres by the branched nerve cells found in the thalami. The thalami are connected by a commissure of grey matter, of which they are largely composed. The corpora striata, which are large oval bodies, are connected posteriorly with the optic thalami, and with the cerebellum, through some of the fibres forming the superior peduncles of that organ; inferiorly with fibres forming the anterior part of the peduncles of the cerebrum; and superiorly and laterally with the grey matter of the cerebrum itself. In their substance, in addition to what is generally diffused, at least three distinct nuclei of grey matter have been described. It has been supposed, with some reason, that the thalami represent the posterior, and the corpora striata the anterior, portion of the cord.

e. *The Cerebrum.*

The hemispheres form an ovoid mass, covering, in man, all the structures already alluded to. The surface is composed of grey matter moulded into convolutions. Each hemisphere has five lobes, the frontal, parietal, occipital, temporo-sphenoidal, and central. It is important to observe (1) the general arrangement of the fibres; and (2) the general structure of the grey matter.

1. *General Arrangement of the Fibres.*—These are divided into three sets—peduncular, transverse, and longitudinal.

a. *Peduncular.*—These, forming the peduncle or crus, consist of fibres derived from the anterior pyramid of the medulla, which probably have ascended from the anterior and lateral columns of the cord; of fibres originating in grey matter of the medulla and of the pons; probably also of fibres connected with those in the pons forming the middle peduncle of the cerebellum; of fibres derived from the corpora quadrigemina, probably continuous with those in the superior peduncle of the cerebellum; and of fibres originating in the grey matter of the corpora quadrigemina. Thus, the hemispheres are intimately connected with the cord, medulla, cerebellum, pons, and corpora quadrigemina.

b. *Transverse.*—These are fibres uniting the *two* hemispheres, consisting chiefly of a great band called the corpus callosum. The corpora striata and optic thalami are also united by transverse fibres.

c. *Longitudinal.*—These, consisting of the fornix, taenia semicircularis, striæ longitudinales of the corpus callosum, gyrus fornicatus, fasciculus uncinatus, and collateral fibres of the convolutions, are for the purpose of uniting physiologically portions of the *same* hemisphere.

2. *General Structure of the Grey Matter.*—The fibres which

form the peduncles, reinforced by many which originate in the grey matter of the corpora striata and thalami, radiate outwards towards the surface of the hemispheres, forming the *corona radiata* of Reil. On the surface of the convolutions, and connected with the fibres just mentioned, there is a layer of grey matter, consisting of several strata. A thin vertical section of this grey matter, stained with carmine, shows six or seven alternate strata, of grey and white matter, not distinctly differentiated from each other, as in the cerebellum, but blending by imperceptible gradations. The white layers consist of minute nerve fibres mixed with a few granules, and imbedded in neuroglia. The grey layers are formed of neuroglia, fibres, and characteristic nerve cells. Of the latter, there are at least three distinct varieties: (*a*) small *granular* cells, very similar in appearance to those forming the granular layer of the cerebellum; (*b*) *pyramidal* or *tripolar* cells, considerably larger than those of (*a*), but very various in size, having the apices of the pyramids directed towards the surface of the brain and minute nerve fibres originating from each angle, and often one springing from the centre of the base; and (*c*) a few large *multipolar* cells, similar in appearance but smaller than those found in the cord. The uppermost layers of grey matter contain only those of *a*; the middle layers contain those of *a* and *b*; whilst those of *c* are only found sparingly along with *a* and *b* in the deepest layers. All of these cells are nucleated.

Full details as to these structures are given in QUAIN, vol. II., p. 558. Consult also LOCKHART CLARKE'S papers in the Proceedings of the Royal Society, 1863, and MEYNERT'S most obscure but suggestive article on the Brain of Mammals, in STRICKER'S Human and Comparative Histology, vol. II., p. 367.

B.—FACTS REGARDING THE PHYSIOLOGY OF PARTS OF CERBBRO-SPINAL AXIS DERIVED CHIEFLY FROM EXPERIMENT AND OBSERVATIONS OF DISEASE.

1. FUNCTIONS OF THE SPINAL CORD.

The spinal cord acts in two ways: (1) as a transmitter of motor and sensory, or centrifugal and centripetal, impressions between the encephalon and the periphery; and (2) a reflex centre.

a. *Transmission of Motor or Centrifugal Impressions.*

Recollect that the anterior roots of the spinal nerves pass into the antero-lateral columns, and that these roots have been proved to be motor. If the anterior columns be cut by an incision extending into the grey matter, leaving the posterior columns intact, voluntary movements disappear in the parts below the section. Again, section of the posterior columns and grey matter, leaving the anterior uninjured, enfeebles but does not destroy the power of voluntary motion below the section. Finally, section of an antero-lateral column on one side paralyses voluntary motion on the same side. From these facts, we infer (1) that the motor tracts passing from the brain to the periphery are in the antero-lateral columns; and (2) that in the cord, the fibres forming these tracts are distributed to the same side of the body. Vulpian has shown that excitation of one anterior column causes movements in the muscles on the *opposite* side. If this be so, there must be a partial decussation of motor fibres in the cord, but it is a doubtful experiment.

b. *Transmission of Sensory or Centripetal Impressions.*

The posterior roots of the spinal nerves pass into the posterior columns and into the grey matter in the posterior cornua. These roots have been proved to be sensory. A complete transverse section of the posterior columns does not abolish sensibility in the parts below; but there is a loss of the power of co-ordinated movements. Section of the posterior columns and of the antero-lateral columns, leaving only the grey matter in the centre of the cord intact, does not abolish sensibility. Again, section of the antero-lateral columns, and of the whole of the grey matter, leaving only the posterior columns uninjured, is followed by complete loss of sensibility in the parts beneath. The inference therefore is that sensory impressions must be conducted in the grey matter. It is manifestly impossible to cut the grey matter, without also injuring the columns; but by a process of exclusion, such as has been followed above, the proof is complete. Brown-Séquard has also found that sensory tracts decussate to a considerable extent in the posterior part of the cord. Thus he found that a hemisection of the cord, involving the grey matter, enfeebled sensibility *on the opposite side* more and more as the section became deep; that a vertical section in the posterior median fissure caused loss of sensibility on both sides; and that a lateral section, whilst it caused loss of sensibility (anaesthesia) on the opposite side, was followed by increase of sensibility (hyperaesthesia) on the same side, a curious fact explained by Brown-Séquard by considering it as due to irritation caused by vaso-paralytic distension of the vessels of the cord on the side of the section. According to him, also, tactile impressions pass in the anterior part of the grey matter, impressions of pain in the posterior and lateral portions, those of temperature in the central part, and those of muscular sensibility in the anterior cornua. Schiff is of opinion that tactile impressions pass in the posterior cords.

c. *The Spinal Cord as a Reflex Centre generally.*

The general character of reflex motions has been already described at p. 177. The grey matter of the lower cervical, dorsal, and lumbar regions of the cord may be regarded as composed of groups of reflex centres associated with the general movements of the body; whilst in the upper cervical region and in other portions of the cord there appear to be differentiated centres corresponding to special actions. The initial excitation may commence in any sensory nerves passing to the cord or in sympathetic filaments. When the impression reaches the cord, a minute interval of time elapses before a muscular response is given. This response may consist either in the movements of muscles specially co-ordinated to a particular centre, or in more general movements of groups of muscles. So exact may the co-ordination be as to produce movements simulating those of a conscious or voluntary character. Thus, in a decapitated frog, irritation near the anus will invariably cause movements of the limbs towards the irritated point. The reflex excitability of the cord is increased by removal of the influence of encephalic centres, as by decapitation, or, in normal circumstances, during sleep, or while the mind is in abstraction or reverie. It may also be influenced by various drugs. Strychnia and the alkaloids of opium increase, while aconite, hydrocyanic acid, ether, chloral, and chloroform have an opposite effect. The precise mechanism in the cord by which a reflex act occurs is unknown.

d. *Special Reflex Centres in the Cord.*

1. *A Cilio-spinal Centre,* associated with the movements of the iris, exists between the sixth cervical and third dorsal nerves. From this region, those fibres in the sympathetic

which control the radiating fibres of the iris originate. If this region be irritated, the pupils dilate, an effect not produced, however, if the sympathetic nerves have been previously cut.

2. *Accelerating Centres*, connected with cardiac movements; see p. 333.

3. *Respiratory Centres.*—Section of the cord above the eighth dorsal paralyses the abdominal muscles; above the first dorsal, the intercostals; above the fifth cervical, the serratus magnus and the pectorals; and above the fourth cervical, by paralysing the phrenics, arrests the action of the diaphragm. These are the general facts, but doubt still exists as to the exact position of these respiratory centres.

4. *Genito-spinal Centre.*—The centre associated with movements of the genital organs, according to the experiments of Budge and Goltz, exists in the lumbar region. The latter observer made the remarkable observation that the activity of this centre may be affected by sensory impressions transmitted by other channels than the ordinary sensory nerves of the parts.

5. *Ano-spinal* and *Vesiculo-spinal Centres.*—These, for the sphincter ani and for the bladder, appear to be in the lower portion of the dorsal, or upper part of the lumbar region.

e. *Supposed Psychical Actions of the Cord.*

Pflüger and others, from experiments on frogs, have supposed that the cord may also be the seat of a low form of consciousness. For example, if a drop of acid be placed on the hind limb of a decapitated frog, the limb of the same side will be flexed and rub against the irritated part; if now the foot be cut off, the limb of the opposite side will be applied, thus apparently indicating not only co-ordination, but the selection of special means in special circumstances.

It may be pointed out, however, that mere movement is no indication of consciousness. It may be associated with consciousness or it may not. Many living objects, such as plants, infusoria, &c., move, to which we cannot, by any stretch of the imagination, attribute consciousness, at least in the sense in which it is used as expressing a mental state. In watching movements of animals deprived of the brain, or of human beings unconscious during disease, an observer is very apt to accept his own interpretations of the phenomena for the phenomena themselves. Thus the movements of a decapitated animal, or the tossing of the hands, wiping of the lips, and the groans and sighs of a person in a comatose state, are regarded as expressions of suffering or distress. Again, when we consider how absolutely dependent consciousness is on a due supply of blood, at all events in the higher animals, can we imagine the molecular actions resulting in this condition to take place in the bloodless cord of a frog? It is, no doubt, true that even the grey matter of a cold-blooded animal, like the white matter, may retain its activity for a time after removal of blood. Without, however, speculating on what may occur in a frog, of whose conscious states we have no knowledge, we have evidence of a different kind from observations on man. In cases of complete paralysis of the lower limbs, either from softening or from the result of accident, the patient may be quite conscious, but he has lost the power of voluntary movement of his legs, and he feels no pain. If the foot be tickled, the legs may move, but there is no indication of consciousness, and the patient expresses surprise at feeling no pain, and at not being conscious of voluntary effort. It may be said that he could not possibly do so, as all communication between the brain and the cord had been cut off, and we are still asked to believe that the movement may have been associated with consciousness in the cord. It is surely much more rational to hold that the movement was purely automatic and unassociated with any conscious state. The author holds that a conscious state is a special form of nervous activity occurring in the higher centres alone. The automatism of the cord is another kind of activity.

2. Functions of the Medulla Oblongata.

Like the spinal cord, the medulla may be regarded as containing tracts for sensory and motor transmission, and as constituting a series of reflex centres for special movements.

a. *Transmission of Motor or Centrifugal Impressions.*

Motor transmission occurs chiefly in the anterior pyramids, and it is important to note that it crosses or decussates. All the motor fibres passing from one side of the brain which are distributed to the muscles on the opposite side of the body, cross or decussate in the anterior pyramids, whilst those supplying the face cross in the pons. In man, the decussation is complete, but in some of the lower animals examined, it is partial. Thus is it possible to explain how it is that disease, causing rupture of motor fibres, passing say from the right cerebral hemisphere, is followed by paralysis of motion on the left side of the body.

b. *Transmission of Sensory or Centripetal Impressions.*

Nothing very precise is known on this point. Section of one half of the medulla does not cause complete loss of sensibility. As has been seen, the majority of the sensory fibres decussate in the cord, so that both motor and sensory fibres in connection say with the right cerebral hemisphere are connected with the left side of the body, but the first cross in the anterior pyramids of the medulla, and the second cross in the cord. It is probable that the sensory fibres pass up through the grey matter of the medulla.

c. *The Medulla as a Reflex Centre.*

When we consider the comparatively small size of the medulla, nothing is more surprising than the number of centres said by physiologists to exist in it, and one cannot help suspecting that we at present know a few empirical facts, and that the hypothesis by which to explain the seeming complexity of function with simplicity of structure is still wanting. The following centres have been located in this portion of the nervous system:—

1. *Respiratory Centres,* two in number, expiratory and inspiratory, connected with the roots of the pneumogastric nerves. Destruction at once causes cessation of respiratory movements and death (see p. 403).

2. *Vaso-motor Centre,* governing all the smaller vessels throughout the body, so as to keep them in a state of tonus (see sympathetic, p. 367).

3. *Cardiac Centres,* two in number: accelerating, associated with the sympathetic; and inhibitory, connected with the pneumogastric (p. 329).

4. *Centres for Deglutition,* associated with the sensory and motor filaments involved in this process (see p. 241).

5. *Centre for Voice,* probably connected with the external root of the spinal accessory, as explained on p. 492.

6. *Centre influencing Glycogenesis.*—Bernard discovered that a puncture in the floor of the fourth ventricle was followed by the appearance of sugar in the urine. This centre is probably associated with the roots of the vagi and of the vaso-motor centre, 2 (p. 429).

7. *Centre directly influencing Salivary Secretion,* from which originate those fibres of the facial, forming the chorda

tympani and lesser superficial petrosal, which are distributed to the glands (p. 234 and p. 48).

8. *Centre for the Motor Fibres supplying the Face and Jaws.*—These exist, in the facial, for the muscles of the face, and in the motor part of the fifth, for the muscles of mastication.

Further, it must be kept in mind that the medulla receives fibres from the higher centres by which all of the centres just mentioned may be more or less influenced.

3. FUNCTIONS OF THE PONS VAROLII.

In addition to forming a transverse commissural band of fibres connecting the two hemispheres of the cerebellum, the pons contains numerous fibres passing from below upwards, and also nuclei of grey matter.

a. *Transmission of Motor or Centrifugal Impressions.*

Motor transmission occurs principally in the anterior part of the pons. Any unilateral lesion causes paralysis of motion on the opposite side, and paralysis of facial on the same side, a fact to be accounted for by supposing that the roots of the facial decussate in the lower part of the pons, whilst the other motor tracts decussate in the medulla.

b. *Transmission of Sensory or Centripetal Impressions.*

In diseases of the pons, loss of sensibility is a much more rare result than loss of motion, and is always on the opposite side. As we have already seen, sensory impressions cross chiefly in the cord. According to Brown-Séquard, tactile, thermal, and painful impressions pass through the central part of the pons.

c. *The Pons as a Reflex Centre.*

Longet has observed movements of the limbs, and even co-ordinated movements after removal of all parts in advance of the pons. Irritation of the pons causes very severe convulsions, and Nothnagel has termed it the region of cramps, or a convulsive centre. This centre may be excited by excess of carbonic acid or the absence of oxygen in the blood, as seen in asphyxia; and it is in close relation with the other centres, such as those connected with respiration, the pupil, the heart, &c., situated in the medulla.

4. FUNCTIONS OF THE CEREBRAL PEDUNCLES.

These contain both sensory and motor fibres; they are intermediate between the centres already described and the voluntary centres in the brain; and they establish a connection between the cerebellum and the cortical part of the cerebrum. Destruction of one peduncle causes the animal to move to the side opposite the lesion, describing a circle somewhat in the manner of a horse in a circus. It is quite evident that irritation of the cerebral peduncles may cause pain, or movements of various groups of muscles, according to the part irritated.

5. FUNCTIONS OF THE CORPORA QUADRIGEMINA.

As indicated by their anatomical connections, these bodies are in intimate relation with vision. Destruction causes immediate blindness. If, in a pigeon, the encephalon be removed with the exception of these bodies, the iris will still continue to contract on the stimulus of light. On then destroying one of the bodies, the pupil remains immobile. From these facts, it is generally held that from the corpora those fibres originate which govern the circular fibres of the iris, and that they are the centres of the reflex movements of this organ. The corpora also receive visual impressions which may be transmitted upwards to the cerebral hemispheres, causing a luminous sensation; or they may result in co-ordinated muscular movements without sensation. It is only by supposing such a mechanism that we can account for the co-ordinated movements seen in some cases of somnambulism, where the individual is apparently quite unconscious of any external impression, but, with open eyes, guides his movements even in difficult and dangerous situations.

The corpora are also associated with the movements of the eyeball in connection with vision. Ferrier found that electrical irritation causes various movements. He observed that stimulation of the posterior tubercles was followed by distinct cries, and that the movements of the body were so violent as to end in general opisthotonus.

It is difficult to operate on these structures in mammals, and consequently our information has been derived chiefly from experiments on birds. Even in these, there is great risk of injuring the underlying crura cerebri, and thus of vitiating the results.

6. Functions of the Optic Thalami.

It is evident that, from the deep situation of these parts, the results obtained by operative interference are not trustworthy. The method least liable to objection is that of introducing, by means of a very fine syringe, a few drops of a solution of chromic acid, or other chemical substance which will produce local destruction of brain matter, without diffusion. When this was done, neither voluntary movements nor loss of sensibility was observed; and the only phenomenon was that the animal placed his extremities in anomalous positions. This fact accords with the view advanced by Meynert, that the optic lobes represent the centres for the combined movements which are the result of impressions constantly transmitted to them from the periphery of the body. Thus the optic thalami are correlated with the tactile surface as the corpora quadrigemina are with the retina. Tactile impressions transmitted to them excite some kind of unconscious activity resulting in a reflex movement. Motor impressions passing from the thalami probably undergo partial decussation. Injury of these bodies also causes the animal to move round a circle. The view held by the older physiologists regarding the functions of these bodies was, that they constituted sensory ganglia, receiving impressions from below, and transmitting them upwards to the brain; this statement, however, has not been proved.

7. Functions of the Corpora Striata.

These bodies have been generally regarded as concerned in the transmission downwards of motor impressions. When a clot of blood is formed in, say, the right corpus striatum, there is motor paralysis of the opposite side of the body, and according to the size of the clot, the paralysis may affect more or less completely the different groups of muscles. Destruction of the two bodies destroys voluntary movement, but the animal may move forwards as in running. Ferrier observed that when the corpora striata were stimulated by an interrupted current, convulsive movements of the opposite side of the body took place; and when the current was powerful, the side of the body opposite to the side of the brain stimulated was forcibly drawn into an arch. Destruction of the intra-ventricular nucleus of grey matter rendered movements of progression impossible, and the animal performed movements of rotation. Nothnagel destroyed the extra-ventricular portions of the corpora striata of a rabbit, with the result of throwing the animal into a state of complete unconsciousness. He also states that in the corpus striatum of the rabbit there is a point, the *nodus cursorius*, the excitation of which causes the animal to rush forwards. This observation agrees with the statement of Magendi, that when he injured these bodies, the animal seemed to have an irresistible propulsion forwards.

8. Functions of the Cerebellum.

The cerebellum is insensible to mechanical excitations. Puncture causes no indication of pain, but there may be movements of rotation, or twisting of the head to the side. Galvanic irritation, according to Ferrier, caused movements of the eyeballs, and other movements indicative of vertigo.

Section of the middle peduncle on one side causes the animal to roll rapidly round its own longitudinal axis, the rotation being usually towards the side operated on. The results of cutting the cerebellum itself are very characteristic. If the cerebellum be removed gradually from a pigeon in successive slices, there is a progressive effect upon locomotive actions. On taking away only the upper layer, there is some weakness and a hesitation in its gait. When the sections have reached the middle of the organ, the animal staggers much, and assists itself by its wings in walking. The sections being continued further, it is no longer able to preserve its equilibrium without the assistance of its wings and tail; its attempts to fly or walk resemble the fruitless efforts of a nestling, and the slightest touch knocks it over. At last, when the whole cerebellum is removed, it cannot support itself even with the aid of its wings and tail; it makes violent efforts to rise, but only rolls up and down; then, fatigued with struggling, it remains for a few seconds at rest on its back or abdomen, and then again commences its vain struggles to rise and walk. Yet all the while its sight and hearing are perfect. The slightest noise, threat, or stimulus at once renews its contortions, which have not the slightest appearance of convulsions. These effects, first described by Flourens, have been confirmed by all experimenters, and occur in all animals. The results contrast very strongly with those of the much more severe operation of removing the cerebral lobes. "Take two pigeons," says Longet; "from one remove completely the cerebral lobes, and from the other only half the cerebellum; the next day the first will be firm on its feet, the second will exhibit the unsteady and uncertain gait of drunkenness." There is thus a loss of the power of coordination of movement without the loss of sensibility. Lussana has attempted to prove that the effects are owing to paralysis of the muscular sense. He supposes that the animal is unable to perform definite movements because it has no feeling of muscular resistance or of the state of its limbs to guide it. The cerebellum, therefore, is not related exclusively to sensibility or movement, but it establishes between the two such relations as render movements precise. Clinical evidence shows generally that disease of the cerebellum, which is very rare, causes unsteadiness of gait, a tendency to push backwards, and blindness; but there are some remarkable cases on record in which extensive disease has existed without any appreciable sensory or motor disturbance.

Gall and Spurzheim, the founders of the phrenological school, advanced the theory that the cerebellum was connected with sexual functions; but there is no evidence to support it.

In conclusion, therefore, it may be stated that the function of the cerebellum is to co-ordinate the muscular movements of the eyeballs with reference to binocular vision, and of the muscles generally in locomotion; but the mechanism by which this is accomplished is unknown.

9. FUNCTIONS OF THE CEREBRUM.

Flourens and the older observers were aware of the fact that as successive slices of grey matter are removed from the surface of the cerebrum, an animal becomes more and more dull and stupid, until at last all indications of perception and volition disappear. A pigeon in this condition, if carefully fed, may live for many months. The following description, given by Dalton, is so accurate as to merit quotation: "The effect of this mutilation is simply to plunge the animal into a state of profound stupor, in which it is almost entirely inattentive to surrounding objects. The bird remains sitting motionless upon his perch or standing upon the ground, with the eyes closed, and the head sunk between the shoulders. The plumage is smooth and glossy, but is uniformly expanded by a kind of erection of the feathers, so that the body appears somewhat puffed out, and larger than natural. Occasionally the bird opens its eyes with a vacant stare, stretches its neck, perhaps shakes its bill once or twice, or smoothes down the feathers upon its shoulders, and then relapses into its former apathetic condition." Similar observations have also been made on reptiles and mammals, but the latter survive the operation for a comparatively short time. In watching such an animal, it is difficult to divest one's mind of the idea that it still feels and sees and hears. It may be observed, however, that it makes no movement unless stimulated from without. Thus, it may remain motionless for many hours;

but, if pushed, or even gently touched, it will then move. It manifests no fear even when placed in circumstances likely to excite it, and it will walk over the edge of a table, or into the fire, quite regardless of consequences. There is thus no proof that it experiences any sensation in the sense of consciousness of impressions; or, in other words, there is no perception. As well remarked by Michael Foster: "No image, whether pleasant or terrible, whether of food or of an enemy, produces any effect on it, other than that of an object reflecting more or less light. And, though the plaintive character of the cry which it gives forth when pinched suggests to the observer the existence of passion, it is probable that this is a wrong interpretation of a vocal action; the cry appears plaintive, simply because, in consequence of the completeness of the reflex nervous machinery and the absence of the usual restraints, it is prolonged. The animal is able to execute all its ordinary bodily movements, but in its performances nothing is ever seen to indicate the retention of an educated intelligence."

The method of removing a portion of the brain is open to many objections, the chief of which is, that the severity of the operation and the loss of blood may cause such a state of shock as to vitiate any inferences that might be drawn from the facts recorded. A new method, however, has been devised, namely, that of stimulating the nervous centres by electricity, and observing the results. Until recently, it has been accepted by all physiological authorities, that the cerebral hemispheres are destitute of irritability. It was apparently shown by Longet, Majendie, Matteucci, Weber, Budge, Schiff, and others, that irritation of the surface of the hemispheres called forth no muscular movements. It was consequently concluded that the cerebral convolutions over their entire extent were associated with the phenomena of the mind. The method of irritating the surface of the brain, with a weak galvanic current, was first pursued in Germany by Fritsch and Hitzig conjointly, who obtained by means of it certain definite results; and in England, by Ferrier, who employed a feeble interrupted current from an induction machine, and whose researches have been of a very extensive character, and, from their relation to pathology, of the highest interest.

These observers found that the local application of the current to particular areas on the surface of the convolutions gave rise to definite co-ordinate movements of various groups of muscles. Stimulation of one spot was followed by movements in the muscles of the neck, of another by extension of the fore leg, of a third by movements of the hind leg, and of a fourth by movements of the eyeballs and of the muscles of the face. Ferrier, in particular, has mapped out definite areas, the stimulation of each of which causes precise movement; and he has also found convulsions to result from simultaneous stimulation of several. These areas have been termed *motor centres*, and it has been supposed by some that influences pass from them to special groups of muscles in the phenomena of voluntary motions. Other observers have ascertained that removal of one of these areas of grey matter is followed by paralysis or weakening of the muscles which contract on the stimulation of the area. After a time however, if the animal survive, it has been observed that the paralysis gradually disappears, apparently from some other part of the brain taking up the function of that which had been removed. Goltz has succeeded in removing considerable portions of cerebral substance, without hæmorrhage, by means of a strong jet of water, and he found that the operation was followed at first by diminished sensation and voluntary power on the opposite side of the body, and imperfect sight, or even blindness. He states that these phenomena occur whatever part of the brain be removed, and he argues that all the temporary phenomena are "due to the superficial lesions exercising inhibitory influences on the parts of the brain lying between the cerebral convolutions and the spinal cord." He also attributes the recovery which is so frequently seen, especially in those cases where the amount of brain matter removed was not very great, to a kind of educational process. It is evident, therefore, that whilst the accuracy of the facts, as stated by Ferrier, is undoubted, physiologists do not yet agree as to their interpretation.

The general results of pathological and clinical observation have thrown considerable light on the functions of the cerebral hemispheres. The following are the chief facts—(1) inflammation of the membranes (termed meningitis), covering the surface of the brain, especially if it involve the superficial layer of grey matter, causes delirium, and afterwards coma; (2) inflammation at the base of the brain, or involving the white matter, causes paralysis or convulsions; (3) in some circumstances, considerable portions of the grey matter may be cut away by accident, or destroyed by an abscess, or by a tumour, without any marked physiological effects—the individual retaining his mental faculties intact, an occurrence which strongly resembles what Goltz observed in dogs; (4) in some cases, sudden depression of a portion of the cranium into a convolution, or a sudden blow on the head, has either arrested the mental faculties as a whole, or has affected the action of one only, as, for example, the memory; (5) pathological states of the grey matter, such as congestions, softenings, degenerations, or the formation of new products, are always associated with the various forms of insanity, but the exact pathological changes peculiar to each form—for instance, melancholia, as contrasted with mania or dementia—are still imperfectly known.

The doctrine that the cerebral hemispheres may be regarded as composed of an aggregate of organs, each devoted to a particular faculty, has been upheld by phrenologists since the days of Gall and Spurzheim. This doctrine must be kept apart from its empirical application in what may be termed cranioscopy, or the determination of mental peculiarities from the existence of elevations and depressions on the surface of the skull. Cranioscopy, in the hands often of ignorant men, has brought undeserved discredit on the cerebral theory of the founders of phrenology. The present state of opinion is certainly in favour of some such theory, but the mapping out of areas on the convolutions can still scarcely be attempted. Ferrier has argued with great ingenuity that the grey matter on the cerebral surface may be divided into three zones: (1) a posterior, corresponding to the posterior cerebral lobes, for the reception of *sensory* impressions; (2) a middle, in which the so-termed *motor* centres exist, and from which motor impressions issue; and (3) an anterior, corresponding to the frontal regions, containing *inhibitory-motor* centres, which govern or restrain subsidiary centres.

One of the most striking indications of specialization of function in the cerebral matter is given by the condition met with in many cases of paralysis, called *aphasia*. In this state, the patient may be unable to express his thoughts in words, and in some cases he uses the wrong words to express a particular thought. Mere loss of speech may be due to paralysis of the nerves governing the articulating organs, and in this case, the patient may have an idea which he wishes to express in suitable words, but cannot do so, from the failure of his organs of speech. In the other instance, however, the articulating mechanism may be intact, but there appears to be a want of co-ordination between the nervous arrangements of the mechanism and those of the idea. Thus when the patient desires a knife, he may be conscious of the appropriate word which is the symbol of a knife, but he utters the word fork or spoon, often to his great surprise or annoyance. It has been ascertained that in the great majority of these cases, the disease affects the posterior portion of the third frontal convolution on the left side, and is associated with right hemiplegia; but cases have been recorded where the right side of the brain was affected. To account for the predominance of the organ on the left side, it has been suggested that as speech is acquired by practice, in most persons only one side of the brain has been educated for this purpose, namely, the left, which governs the movements of the right, and, in most persons the stronger, side of the body.

10. The Circulation in the Brain.

It is important to remember that a due supply of healthy arterial blood and the removal of venous blood are essential to cerebral activity. The physical conditions of the circulation are also deserving of notice. The brain is contained in an osseous case of which the total capacity is invariable. The cerebral substance undergoes almost insignificant changes of volume even under a pressure of 180 mm. of mercury. The quantity of blood, however, in the cranium may vary. If a small round window be made in the cranium, and a suitable piece of glass be fitted into it, the veins of the pia mater may be observed to dilate or contract if intermittent pressure be made on the veins of the neck. There is evidently then within the cranium some arrangement by which such variations become possible. This is probably accomplished by the anatomical arrangements of the subarachnoid spaces. These spaces, containing fluid, communicate freely with each other, and with the space surrounding the spinal cord, so that when the quantity of blood increases in the cranium, a corresponding quantity of fluid escapes into the spinal space, the walls of which are not inextensible like those of the cranium. In young children, before the fontanelles are closed, the variations of circulation and cerebral pressure cause pulsations of which there are two kinds: those coinciding with the ventricular systole, produced by the pulsation of the arteries at the base of the brain; and those coinciding with expiration. These movements have been registered graphically. No satisfactory account has yet been given of the arrangements by which waste products are removed from the brain.

Consult FERRIER On the Functions of the Brain, 1876; and MICHAEL FOSTER'S Textbook of Physiology, p. 430. Dr. Ferrier's book gives a full and most interesting account (1) of the present state of opinion regarding the physiology of the centres; (2) of his own original researches; and (3) of the conclusions he has been able to arrive at after a survey of the whole field of inquiry. The student of nervous physiology should also read Sect. V. of MÜLLER'S Physiology, translated by BALY, "Of the central organs of the nervous system," vol. I., p. 788. A discussion of various views as to the cranial circulation will be found in BENNETT'S Physiology, p. 220, and p. 289. In the Glasgow Medical Journal for 1877, a paper will be found by W. J. FLEMING, showing tracings of the movements of the brain; also a similar paper, in MAREY'S Physiologie Expérimentale, 1876.

III.—TERMINAL ORGANS AND THE SENSES.

A.—GENERAL CONDITIONS OF SENSORY IMPRESSIONS.

By a sensory impression is understood the effect produced by the action of excitants on the organs of sense, when the effect is consciously perceived. The perception of the impression, and its reproduction as a mental image, are psychical acts, belonging to the province of psychology.

1. Mechanism of Sensory Impressions.

This has been already briefly alluded to on p. 149. The essential conditions are (1) a *terminal apparatus*, for the reception of the excitant; (2) a *nerve*, for conducting impressions to the brain; and (3) a *brain*, or *cerebral ganglion*, for the reception of these impressions. It is important to regard the nerve as simply a conductor. It is the bond of union between the terminal organ and the ganglion. Such nerves are known as nerves of special sensation, because the impressions conducted by them are always interpreted by the mind in a particular way. Thus, the auditory nerve may be stimulated by various excitants, such as pressure, or cutting, or by its normal stimulus from the terminal organ in the ear; but when the impression reaches the brain, it always gives rise to a sensation of sound. This fact, however, does not imply that the fibres of the auditory nerve are necessarily different from those of any other nerve; but only that the central mechanism so acts as to produce this particular kind of sensation. It is remarkable that such nerves are not capable of being excited directly by the stimulus which acts upon their terminal organ. For example, the fibres of the optic nerve are insensible to the action of light, and those of the auditory nerve to sound. It would appear that the normal stimulus which, acting on the retina, or on the organ of Corti, gives rise to sensations of light or of sound, is too weak to affect directly the filaments of the nerve. A terminal organ, therefore, is required to receive the outer stimulus, and to excite the conducting filaments of the nerve. Each organ of sense has a special terminal apparatus peculiar to itself, and adapted for the reception of a special kind of stimulus. The retina is adapted for the action of light, the vibratory apparatus in the ear for the motions of sound, and the modified epithelial structures on the tongue and in the nose for the specific action of soluble substances and odoriferous particles.

It would appear that a sensory transmission does not pass directly to the cerebral hemispheres, which we regard as the seat of conscious perceptions; but that there is a recipient centre, which in the first instance receives these impressions, and which may or may not transmit them to the perceptive centre. This arrangement is most evident in connection with the mechanism of vision, where we find the corpora quadrigemina interposed, as it were, between the cerebral hemispheres and the optic tracts, which are continuations of the optic nerves. These may be regarded as centres for the reception of impressions transmitted by the optic fibres from the retina. As the physical stimulus acting on the retina is a mode of motion in the form of waves of light, it is evident that its action will be intermittent, and that these intermittent impulses, following each other with great rapidity, will be transmitted along the optic fibres. It is not improbable that such impulses may be fused together in the receptive centre, and transmitted as a whole to the cerebrum. It was long ago suggested by Von Græfe, the eminent oculist, that the corpora quadrigemina acted in some such way, and he further supposed that luminous effects might be stored up in these organs, ready to be transmitted to the brain. This view might account for the vividness of some kinds of ocular illusions experienced whilst under the influence of such a drug as Indian hemp, or by the insane. To a conscious mind thus receiving old impressions which had long remained latent, the sensations or conscious perceptions would have all the vividness of reality, and would be just as truly referred to the outer world as if they had been immediately caused by the direct action of light on the retina, or of waves of sound on the ear, *because they reached the perceptive centre along the same channels.*

Such subsidiary cerebral centres also no doubt fulfil the purpose of linking the organs of sense, and the impressions they produce, with motor phenomena. Facts bearing upon this question have already been alluded to in treating of the corpora quadrigemina.

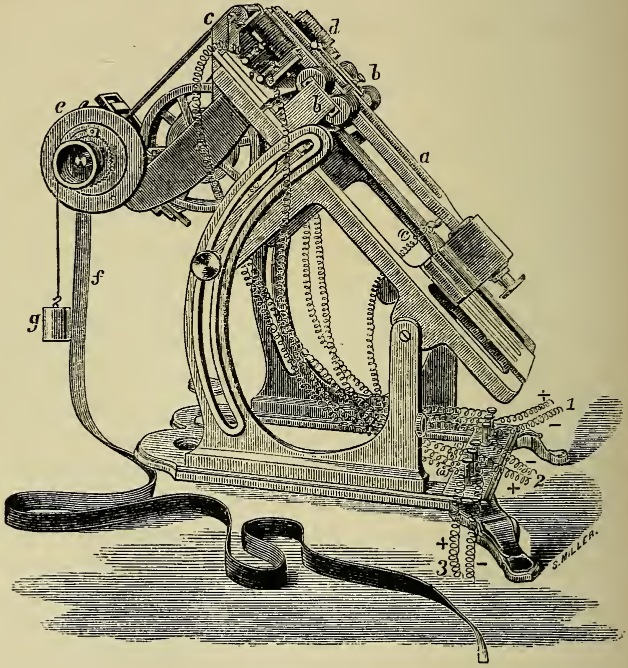


FIG. 132.—Chronograph for the measurement of time in physiological experiments. *a*, tuning fork; *b b*, electro-magnets working it; *d*, electro-magnetic signals; *c*, band of smoked paper rolled off by weight *g*, working the wheel *e*. 1, wires for right signal, *d*; 2, wires working recording fork; and 3, wires for left signal.

2. Time in Sensory Impressions.

It has been ascertained by accurate experiment that sensory impressions, and nervous phenomena of a kindred nature, occurring in terminal organs and in nerve centres, involve expenditure of time. Various methods have been adopted to determine the time with accuracy. The most convenient apparatus for the purpose is a chronograph made by König, which is shown in Fig. 132. It consists of a large tuning fork (see Fig. 133, AA), vibrating 200 periods per second. This is placed in an upright position, and is

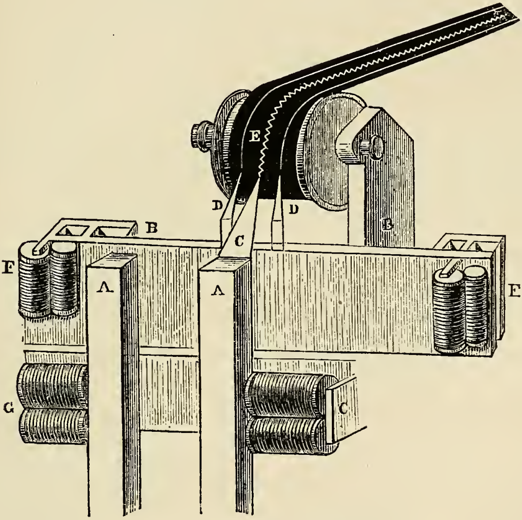


FIG. 133.—Diagram showing the recording portion of chronograph. AA, limbs of recording fork, worked by electro-magnets, GG. C, stylet on limb of recording tuning-fork. BB, levers in connection with armatures of electro-magnets, FF, and bearing markers DD, which, along with C, record on E, a strip of blackened paper passing over pulley.

kept in constant vibration by an electro-magnet placed on the outer side of each limb (GG). In front of a marker (C), placed on one of the limbs of the recording tuning-fork, a thin strip of blackened paper (E) is drawn vertically over a pulley. On each side of this vertical tuning-fork, and on a level with its marker, is another electrical apparatus, consisting of an electro-magnet (FF), the armature of which is prolonged, and carries a marker (DD), which is on an exact level with that of the tuning-fork. When a current passes through the coil the armature descends, and the moment is indicated by a mark on the blackened paper. One marker, say the one to the left, is employed to signal the instant of the application to a sense organ of a physical stimulus, say light on the eye, or an electric shock to the skin, while the other, say the one to the right, is set in action by the individual receiving the stimulus immediately opening or closing the key interposed in the circuit. To make the matter intelligible, a diagram of the recording part of the apparatus is shown in Fig. 133.

Suppose it were wished to measure the time between the moment of stimulating the skin of the hand by an induction current and the moment of signalling back that the impression had been received, the apparatus is arranged as seen in the next figure. The chronograph *a* is placed somewhat obliquely, and not vertically, as shown in the figure. The recording fork is worked by a current transmitted by the wires *i*. In the circuit of the Daniel's cell, *b*, the primary coil of the induction machine, *d*, and the left electro-magnetic signal of the chronograph are placed—a key, *c*, being also interposed in the circuit. When the key *c* is closed, the current is passed through the electro-magnetic signal so as to work the marker, and the instant is recorded on the band of smoked paper. By the closing of the same current, a shock is sent from the secondary coil *e* to the left hand of the observer, *h*. The instant he feels the shock, he closes the key *g*, interposed in the circuit of the Daniel's cell *f*, the current of which passes through the right signal of the chronograph, and the instant of the closure of this current is also recorded on the smoked paper. When the apparatus is all arranged, the band of smoked paper is rolled rapidly in front of the markers by the weight *k* being allowed to fall to the ground; the key *c* is closed, the observer feels the shock, closes the

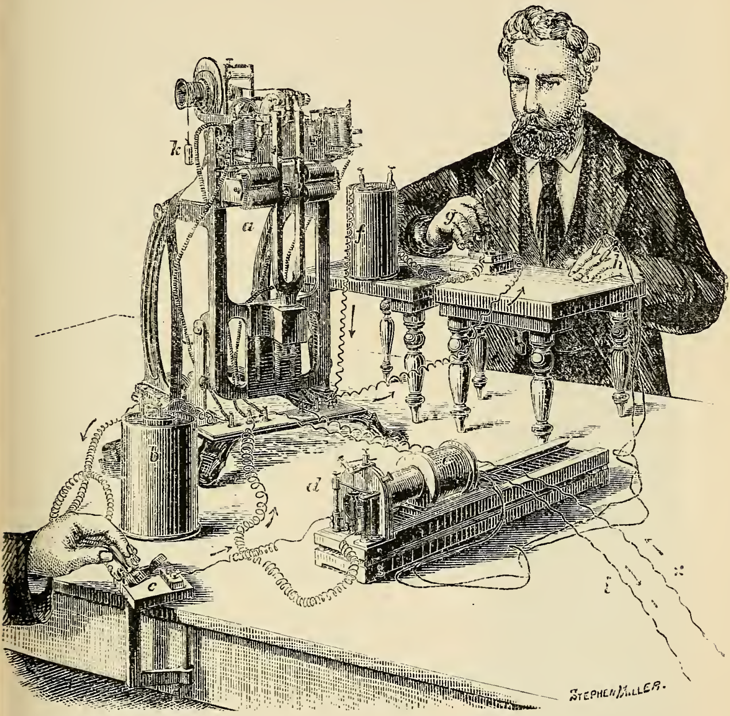


FIG. 134.—Arrangement for measuring the time required for receiving a sensory impression, and indicating by muscular action that it has been received. *a*, Regnault's chronograph; *b*, Daniel's cell, in primary coil of induction machine *d*, the current being interrupted by the key *c*; *e*, secondary coil of induction machine, by which a shock is sent to the hand *h* when the key *c* is opened. On receiving the shock, the person operated on closes the key *g* in the circuit of the cell *f*, and the instant is signalled by the chronograph. For further description see text.

key *g*, and the time of the phenomena is recorded on the paper, as shown in tracing, Fig. 135.

It is evident that an interval of time must elapse between the moment the shock is given and the moment the observer signals that he felt it. Suppose in the tracing shown in Fig. 135, that time is recorded by the fork's vibrations in the line C; that the instant the shock was given is indicated by the line A being drawn inwards by the electro-magnetic signal at *a*, and that the instant the impression is received is indicated by the inflection of the line B at *b*: the interval of time between the moment of stimulus and the moment of signalling that it was felt is shown by the length of the line *a b*, found by drawing the dotted horizontal lines. By counting the number of the fork's vibrations in that distance, the time may be ascertained; thus, as in the diagram, $\frac{8}{200}$ of a second = $\frac{1}{25}$. (In like manner, the time required to perceive lights of various colours may be measured by sending an instantaneous induction shock through a Geissler's vacuum tube.) During the time so registered, various phenomena occur. The shock irritates sensory structures in the skin of the hand; the influence so excited travels along the sensory nerves with a certain velocity; sensation and perception occur in the brain; there is then a volitional impulse; an impression travels along the motor nerves to the muscles of the arm; and, finally, time is occupied by the contractions of these muscles.

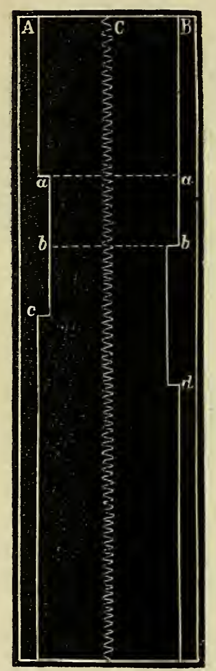


Fig. 135.—Tracing obtained with the chronograph.

The following are the general results thus obtained by physiologists:—

Nature of Stimulus.	Time between application of stimulus and signal of perception in fractions of a second.	Name of Observer.
Shock on left hand, . . .	·12	Exner
Shock on forehead, . . .	·13	Do.
Shock on toe of left foot, . .	·17	Do.
Sudden noise, ...	·13	Do.
Visual impression of electric spark,	·15	Do.
Hearing a sound, ...	·16	Donders
Current to tongue causing taste, .	·16	Von Wittich
Saline tastes, ...	·15	Vintschgau and Hönigschnied
Taste of Sugar, ...	·16	Do.
,, Acids, ...	·16	Do.
,, Quinine, ...	·23	Do.

It has also been ascertained by such methods that the time is much prolonged when a *decision* has to be arrived at as to the part stimulated, or as to the mode in which the response is to be given, thus showing that the element of time enters into purely mental operations.

3. Relation between the Stimulus and the Impression.

The stimuli which act on our sense organs are movements of various kinds. Thus, light is caused by vibrations of ether, sound by movements of the air, and touch is due to oscillations either of the body touched or of the skin touching it. In all periodic movements of the character of wave motion, three points are to be noted: (1) the *length* of the wave, determining the number of waves in a unit of time; (2) the *amplitude* of the wave affecting the intensity of the impression; and (3) the *form* of the wave which must have an influence on the kind of effect produced. This will be illustrated in treating of hearing.

4. Relation between the Stimulus and the Sensation.

1. *Intensity of Sensation.*—Suppose some mode of energy, such as sound or light, to act on a terminal organ, the stimulus might be so weak as to produce no sensation; by increasing the strength of the stimulus to a certain point, a very feeble sensation would be experienced—that is to say, a *lower limit of excitation* has been reached. On further increasing the intensity of the stimulus, it will be found that the intensity of the sensation is also increased, according to a law which has been thus formulated in general terms by Fechner: "When the intensity of the sensation increases, according to absolutely equal quantities, the energy of the excitation also increases according to relatively equal quantities." For the sake of clearness, this law may be expressed in another way. The intensity of a sensation depends on two conditions: (1) the intensity of the excitation, and (2) the degree of excitability of the sensitive organ at the moment of excitation. It has been found that the intensity of the sensation does not increase proportionately to the intensity of the excitation. Thus, we have a luminous sensation of a certain intensity if a lighted candle be brought into a dark room, but the introduction of a second candle does not double the intensity of the sensation, but increases it only to a slight extent, whilst a third candle produces no appreciable effect. By varying the absolute amount of the stimulus, and noting the corresponding strength of the sensation, it has been found that when the stimulus is doubled, tripled, quadrupled, &c., the sensation does not increase correspondingly, but *it increases as the logarithm of the stimulus.* Thus, suppose the excitation to be 10, 100,

1000 times increased, the sensation becomes only 1, 2, or 3 times more strong.

In sensory impressions we have: (1) a *minimum of excitation*, that is, the smallest excitation capable of producing a sensation; (2) a *maximum of excitation*, beyond which no increase in the amount of the stimulus augments the intensity of the sensation; (3) a *constant proportion or ratio* between the intensity of the excitant and the intensity of the sensation, governs sensory impressions between the lower and the upper limits (Law of Fechner). The constant ratios for each sensation also express the least perceptible difference between two sensations. Suppose, with the eyes blindfolded, a weight of 10 grammes to be placed in the palm of the right hand; there is a sensation of weight of a certain intensity; to alter this sensation, by diminishing it, 3·3 grammes will have to be removed before a difference is perceptible, or, by increasing it, 3·3 grammes must be added to it. Again, with 100 grammes, 33·3 grammes, and with 1000 grammes, 333·3 grammes, before appreciable differences will be observed—that is to say, the added or subtracted weight will be in the ratio of 1 : 3 with the primitive weight. The ratio 1 : 3 = the *constant proportion.* The following table gives the constant proportion for each sense:—

Tactile sensations, ...	1 : 3
Sensations of temperature, . . .	1 : 3
Auditory sensations, ...	1 : 3
Muscular sensations, ...	6 : 100
Visual sensations, ...	1 : 100

The following are the values of the *minimum of excitation* for the different senses:—

Sensation of touch: pressure of ·002 grammes to ·05 grammes. (*Aubert.*)

Sensation of temperature: $\frac{1}{8}$ of a degree C.; the temperature of the skin being about 18·4° C. (*Weber.*)

Sensation of movement: shortening, to the extent of ·044 millimetre, of the internal rectus of the eye. (*Wundt.*)

Sensation of sound: a ball of pith, 1 milligramme in weight, falling 1 millimetre in height, upon a glass plate, may be heard at a distance of 91 millimetres from the ear. (*Schafhäutl.*)

Sensation of light: an intensity of light about 300 times more feeble than that of the full moon. (*Aubert.*)

2. *Quality of Sensation.*—We may assign different qualities either to sensations of different senses, or to sensations of the same sense caused by different forms of excitation. Thus the quality of an auditory, is different from that of a visual, sensation, and the quality of the sound of a piano is different from that of the human voice. The contrast between auditory and luminous impressions, as regards their respective excitants, is striking. Both are caused by movements, but the lowest sound audible as a musical tone is caused by 16 vibrations per second; the highest sound audible to the ear by 36,000; while the sensation of red at one end of the spectrum corresponds to 450, and that of violet at the other end to 785, *billions* of vibrations per second. Sensations of temperature are caused by vibrations which come in far above the range of audible sounds, and approach, and blend with, the lower limits of those causing luminous impressions. It is not possible, in the present state of science, to make definite statements as to the molecular movements causing touch, taste, and smell.

3. *Objectivity of Sensory Impressions.*—When a nervous impression from a terminal organ reaches the brain, it excites in it changes which result in a *sensation;* and if the sensation be referred to some cause outside of the body,

there arises what may be termed an *idea*. The link between the sensation, considered in its simplest form, and the idea, may be spoken of as a *perception*. Regarding the mechanism of these processes we know nothing. They may all result from the same kind of nervous activity, but of different degrees of intensity, or they may be related to broader areas of grey matter. Thus a feeble stimulus may produce such actions as result in mere sensation; a strong stimulus may cause perception; whilst a third may result in an idea of the cause of the stimulus. As has been pointed out by George Henry Lewes, the term sensation has been applied to very different things; we need a word which will express that lower form of nervous activity which may result in automatic movements, or which, in other circumstances, may be associated with conscious perception.

Sensations of sight, of hearing, and to a feebler extent, of smell, are projected into the external world, whilst those of touch and taste are referred to the periphery of the body. In addition, there are numerous ill-defined sensations, such as desires, feelings of hunger or of satiety, pleasurable or stifled respiration, the langour felt in breathing an impure atmosphere, &c., which we are unable to refer to any particular place. Sometimes, in the organ of vision or of hearing, exciting causes operate in the organ itself, so as to give rise to sensations, which are referred to the exterior. Such are the dots sometimes seen dancing before the eye, and the blowing, buzzing, and ringing sounds which may distress the ear during disease. In all probability, the projection of visual and auditory sensations is partly to be explained by habit and partly by supposing that it may be due to reasoning processes by which phenomena are connected with their causes.

For details regarding these interesting psychological questions see Wundt's Psychologie Physiologische; also his Physiologie, p. 441.

Consult also George Henry Lewes, Physical Basis of Mind, and his History of Philosophy, in which he gives in great detail the views of many authors; Herbert Spencer's Principles of Psychology; Fechner's Elemente der Psychophysik; Taine, on Intelligence; R. S. Wyld, the Physics and Philosophy of the Senses; Delbœuf, Recherches Théoriques et Expérimentales sur la Mesure des Sensations; Bain, the Senses, and the Emotions and the Will; James Sully's Sensation and Intuition; and various articles by Wundt, Sully, and Lewes in "Mind" for 1876 and 1877.

B.—*THE SENSE OF TASTE.*

1. Anatomical Conditions.

The tongue is the essential organ of taste, but the upper part of the anterior surface of the soft palate, and probably the anterior pillar of the fauces, are endowed with gustatory sensibility to a feeble extent. The nerves connected with this sense are (1) the glosso-pharyngeal supplied to the posterior third; (2) the lingual branch of the fifth distributed to the anterior two-thirds; and (3), according to some authorities, filaments in the chorda tympani. These nerves are distributed to the papillæ on the surface of the tongue, of which there are three varieties—the simple or filiform,

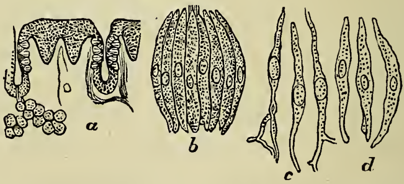


Fig. 136.—Organ of taste from tongue of rabbit: *a*, section through *taste organ*, showing flask-shaped bodies in the depressions; *b*, flask body isolated, showing that it is made of spindle-shaped cells; *c*, small cells found in flask, having pointed lower ends which are continous with nerve fibres; *d*, fusiform cells which form wall of flask-shaped body,

the fungiform, and circumvallate. In the latter, as found in the tongue of the rabbit, special terminal organs have recently been discovered, which are shown in Fig. 136.

2. PHYSICAL CAUSES OF TASTE.

The organ is excited by substances in solution, which may be classified, according to the sensation they excite, as salines, sweets, acids, and bitters. Such substances as cayenne or mustard do not give rise to pure sensations of taste, but act chiefly on the tactile sensibility of the tongue as irritants. Colloidal substances, such as albumen, are devoid of taste; and the sensation can only be excited by crystalloids readily soluble in water, or in the fluids of the mouth. No definite relation can be established between the chemical constitution of a substance and its gustatory properties. Thus substances so different as sugar, the salts of lead, and chloroform, are all sweet. It is remarkable that mineral substances containing 3 atoms of O to 2 atoms of the base, such as Al_2O_3, Fe_2O_3, and hyposulphites are usually sweets, whereas vegetable alkaloids are bitters. The sensation of taste may also be excited by a slender but powerful current of cold air driven against the tongue, and by electrical stimulation.

3. PHYSIOLOGY OF TASTE.

The base of the tongue is the region most sensitive to bitter substances, whilst the point is most affected by sweets and acids. Taste depends physiologically on the contact of the soluble matter with the terminal organs, which are situated in the papillae. No sensation is experienced when the substance is placed between two papillae. The sense may be excited by the presence in the blood of bitter substances, a fact which may account for the intensely bitter taste experienced during jaundice. As regards sensibility to taste, there can be no doubt it is most acute for bitter substances. One part of sulphate of quinine in 100,000 parts of water is still perceptible. What we term tastes, in ordinary language, are frequently sensations of a compound character, due partly to gustatory and partly to olfactory impressions. For example, if the nostrils be held firmly, it is impossible to distinguish between the sensations produced by applying an onion or an apple to the tongue. The sense may, in cases of disease, be paralysed without interference with tactile sensibility, and the reverse has also been observed.

C.—SENSE OF SMELL.

1. Anatomical Conditions.

The organ of the sense of smell is the mucous membrane lining a part of the nasal cavities supplied with nerves from the *olfactory* bulbs or first pair of cranial nerves. Attached to the side walls of each nasal cavity are two delicate scroll-like bones, called *turbinated* bones, which to a great extent divide each cavity into three spaces, lying one above the other. The uppermost two of these constitute the true olfactory chambers, whilst the lowest passage is merely used for respiratory purposes. The whole of this bony framework is covered by moist mucous membrane, having imbedded in it flat elongated cells attached to the ramifications of the olfactory nerves (Fig. 137). By the contact of certain substances with these, a sensation of smell is produced.

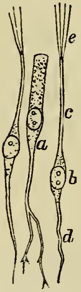


Fig. 137.—Cells from the olfactory organ of two kinds—*a*, with broad ends like knife-handles; *c*, with delicate pointed ends, and continuous with nerve-fibre at *d*.

2. PHYSICAL CAUSES OF SMELL.

These are substances present in the atmosphere in a state of extremely fine subdivision, or existing as vapours or gases. Graham pointed out that odorous substances are in general readily oxidized. For example, sulphuretted hydrogen, the ethers, alcohols, and essential oils have this property; and, on the other hand, such a gas as light carburetted hydrogen, which is not acted on by oxygen at ordinary temperatures, has no odour. The fine state of subdivision of odoriferous bodies is illustrated by the fact that a grain of musk can affect the atmosphere of a room of considerable size for years without appreciably losing weight, and that 1 part of H_2S in 1,000,000 parts of air may be distinctly perceptible. Venturi and Liégeois have studied the physical movements of odoriferous particles, such as camphor, succinic acid, &c., when placed on the surface of water; and among other interesting facts they have ascertained that the materials forming essential oils may cause a film on the surface of water of almost inconceivable thinness. It is well known that the odours of flowers are most distinctly perceived in the morning, or after a shower, when the atmosphere contains a considerable amount of aqueous vapour. It would appear also that the odours of animal effluvia are of higher specific gravity than the air, and do not readily diffuse; a fact which may account for the pointer and bloodhound keeping their noses to the ground.

3. THE PHYSIOLOGY OF SMELL.

Smell is excited by the contact of odoriferous particles with the mucous membrane of the nose. It is necessary that the air containing the odour be driven forcibly against the membrane. Thus, smell only occurs when the air is drawn into the nostrils, and one may enter a room, the air of which is impregnated with H_2S, and experience no odour if he does not breathe. Another condition of the sense of smell is that, under the action of the same odour, it diminishes quickly in intensity. The first scent of a rose or of a perfume is the strongest and sweetest; and after a few minutes' exposure, the intensity of even a fœtid odour may not be perceived. This fact may be accounted for on the supposition that the olfactory membrane becomes quickly coated with a thin layer of matter, and that the most intense effect is produced when the odoriferous substances are applied to a clean surface. The delicacy of the sense is much greater in many of the lower animals than in man, and it is highly probable that the dog or cat obtain information by means of this sense which a human being cannot get. Such animals make a much greater use of the sense than the human being, and it is not unlikely that odours may produce in their minds more vivid impressions, which also may be recalled by acts of memory. The sense of smell in man may be increased by education. A boy, James Mitchell, was born blind, deaf, and dumb, and chiefly depended on smell for keeping up a connection with the external world. He employed it on all occasions, like a domestic dog, in distinguishing persons and things. In some rare cases, the sense of smell is entirely absent in human beings.

Of the exact changes undergone by the odoriferous particles, nothing is known.

Odour may give information as to certain characters of food and drink, and as to the purity of the air. In the lower animals, also, the sense is associated with sexual functions.

D.–THE SENSE OF TOUCH.

1. Anatomical Conditions.

The organs of touch are situated in the papillæ of the true skin and in a few other places. They are of three kinds: (1) *end-bulbs*, found in the glans penis, and in some of the papillæ in the red border of the lips, consisting of a small capsule of connective tissue containing soft matter, in which one or more fibres of a nerve terminate; (2) *touch-bodies*, found in certain papillæ of the palm and sole, more sparingly in those of the back of the hand and foot, the palmar surface of the fore-arm and nipple, formed of a core of soft material enclosed by a firm capsule of connective tissue, which is surrounded by a few coils of nerve fibre, the fibre ultimately entering into an aperture at the apex of the oval structure; and (3) *Paccinian bodies*, like small seeds, attached to the branches of nerves as they pass through the subcutaneous fat on their way to the skin, and consisting of a series of concentric layers of connective tissue, enclosing a transparent soft substance in which the termination of the nerve is imbedded. The latter structures have frequently been found in the mesentery, and as they are situated more deeply than the other two bodies, it has been supposed that their special functions may be connected with sensations of pressure.

2. Physical Causes of Touch.

Sensations of touch are caused by mechanical actions, such as contact, pressure, or traction applied to the sensory nerves of the skin. Solid bodies act either by pressure or by traction. As regards pressure, it may be so slight as to give rise simply to a sensation of contact, or it may be so great that a new sensation, that of pain, is developed. It may also vary not only as regards intensity, but in extent; it may be uniform or irregular. It would appear that continuous pressure, even when gentle, will not give rise to a sensation of simple contact or touch, so that *inequality* of pressure is one of the conditions of tactile sensations. Thus a mould of paraffin on the tip of the finger, when it solidifies, gives rise to no tactile sensation, as it presses equally upon all points of the skin. Tickling is caused by very gentle contacts succeeding each other rapidly over a surface of some extent, so as to irritate numerous fibres. Traction, as on pulling a hair, gives rise to a sensation which may gradually pass from a simple feeling of contact to pain. Fluids press uniformly on all parts of the cutaneous surface, with the exception of the part in contact with the surface of the fluid. There is thus, when the fore-finger is dipped in mercury, no feeling of contact in the part of the finger in the air or in the part immersed in the mercury, but only a sensation of a ring at the level of the surface of the mercury. A current of cold gas gives rise to a tactile sensation when it strikes the surface of the skin obliquely.

3. PHYSIOLOGY OF TOUCH.

The anatomical arrangements for the sense of touch are evidently for the purpose of communicating delicate movements to the extremities of the sensory nerves. This is accomplished by having the delicate extremities of the nerves imbedded in a semi-fluid substance, surrounded by a tolerably firm but elastic capsule. It has occurred to the author that such an arrangement would facilitate the transmission of oscillations to the ends of the nerves. Such oscillations constantly occur in the body itself, probably from feeble muscular tremors combined with the influence of the elasticity of the parts. If a marker be attached to any part of the body, and more especially to the extremities, and be brought in contact with a rapidly moving surface, such tremors may be seen graphically, although the individual is not conscious of their existence, and although they cannot be followed by the unaided eye. If this be the case, when the tip of the finger touches the table, it is not motionless, but oscillates through minute distances, and these oscillations are communicated by the elastic touch-bodies to the ends of the nerves. Meissner has advanced a similar hypothesis. It has been ascertained also that if we apply the tip of the finger to the teeth of a rapidly rotating wheel, when it receives about 640 shocks per minute, the sensation is fused into one of contact with a considerable amount of pressure.

a. *Sensations of Contact.*—These may vary with the nature and intensity of the excitant, and with the extent of surface excited. It is difficult to vary the nature of the excitant without at the same time calling agencies into play which are not properly connected with touch. Thus, if we touch a body at different temperatures, different sensations may be experienced. Again, if we touch a body it may feel cold or warm, according as it is a good or a bad conductor of heat. Here we have sensations of temperature as well as tactile sensations. At the same time, bodies of the same temperature, such as a bit of wood, a fat, a fluid, or a jet of gas, may give rise to tactile sensations of different quality. The sensation may be soft or hard, smooth or rough, oily or astringent. Again, if two parts of the skin of the body touch each other, we refer the sensation chiefly to the most sensitive. Attempts have been made to measure the delicacy of sensations of contact by means of small weights. Thus, it was found that a weight of 2 mgm. pressing on 9 square mm. of cutaneous surface was sufficient on the forehead, temples, and nose; 3 on the palm of the hand; and 15 on the palmar surface of the index finger.

b. *Compound Tactile Sensations.*—When two points on the skin are touched simultaneously, we may have two sensations; but if the points be brought in very close proximity, the two may be fused into one. Taking advantage of this fact, H. Weber determined the sensitiveness of different regions of the skin by applying the points of compasses, and finding the nearest limit at which the double sensation was experienced. The following are a few of his results in millimetres :—

	mm.		mm.
Point of the tongue,	1·1	Back of hand,	31·5
Palmar surface of third phalanx of fingers,	2·2	Neck, under the chin,	33·7
Red border of the lips,	4·5	Knee,	36·0
Dorsal surface of third phalanx,	6·7	Forearm,	40·5
Middle of tongue,	9·0	Sternum,	45·4
Jaw,	11·2	Side of neck,	54·1
		Back,	54·5
		Shoulder,	67·6

It has been found impossible to distinguish more than 4 or 5 points of contact at once.

c. *Duration of Tactile Sensations.*—The sensation lasts for a short time after cessation of the exciting cause. Therefore, in the experiment with the rotating toothed-wheel before described, the sensation produced by the contact of each tooth must have lasted longer than the $\frac{1}{640}$th of a second.

d. *Localization of Tactile Sensations.*—We know more or less exactly the point that has been touched. Sometimes, however, strange illusions occur, as in the well-known experiment of Aristotle. If we cross the index and the middle finger, and roll about a small marble on the table, there is a sensation of two marbles. It results from the tendency to decompose a sensation into two, and to refer each to the area of skin, from which we are in the habit of receiving impressions of that character.

e. *Influences varying Tactile Sensibility.*—It is dull where the epidermis forms a thick coat, and, as a rule, delicate where it is thin. The presence of the epidermis is necessary, as we find tactile impressions give way to sensations of pain when it is deficient or injured. It may be modified by exercise, which not only increases delicacy of touch, but augments the faculty of localization and of judging pressure. These statements are illustrated by the skilful manipulations of experienced artizans. The educated touch of the surgeon is an instance of an acquired power of combining sensations of contact and of pressure, as indicated by the amount of resistance, and of forming a rapid and accurate judgment.

E.—*SENSE OF VISION.*

1. Anatomical Conditions.

The eye is a nearly spherical organ, formed of transparent parts situated behind each other, and surrounded by various membranous structures, of which the anterior part is also transparent. The transparent parts in the interior of the eye are: (1) the *aqueous humour* found in the anterior chamber of the eye; (2) the *crystalline lens*, formed by a transparent convex body, of which the anterior surface is less convex than the posterior; and (3) the *vitreous humour*, a semi-fluid substance, surrounded by a structureless membrane, the *hyaloid membrane*, situated in the posterior chamber of the eye. The *lens* is formed of a series of layers, which in turn are made up of fibres; and it increases in density from the circumference towards the centre. These transparent parts are surrounded by three layers of membrane, the one outside of the other—(1) an external layer, the posterior part of which is formed by the *sclerotic*, and the anterior part by the transparent *cornea;* (2) the *choroidal* or vascular membrane, composed of the choroid properly so called, which lines the internal surface of the sclerotic, and the anterior part of which forms the

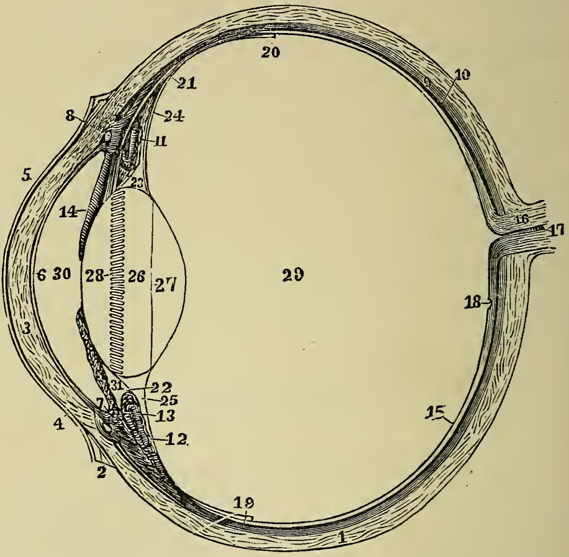


Fig. 138.—Diagrammatic Section of the Eyeball (*Wundt*). 1, sclerotic; 2, junction of sclerotic and cornea; 3, cornea; 4, 5, anterior layer of epithelium (conjunctiva); 6, posterior elastic lamina; 7, 8, junction of iris with choroid; 9, 10, choroid; 11, 12, 13, ciliary processes; 14, iris; 15, retina, lined by hyaloid membrane; 16, fibres of optic nerve; 17, arteria centralis retinæ; 18, yellow spot; 19, 20, anterior portion of retina; 21, 24, membrane passing behind lens; 22, 25, membrane passing in front of lens; 23, canal of Petit; 26, 27, 28, lens; 29, vitreous humour; 30, anterior chamber, containing aqueous humour; 31, space between iris and anterior layer of capsule of lens.

ciliary processes and the *iris*, a movable diaphragm, surrounding an aperture termed the *pupil;* and (3) the *retina*, which lines the posterior part of the eyeball, being placed between the choroid and vitreous humour. The retina, as will be hereafter seen, is the layer sensitive to light; but to reach it a luminous ray must pass from before backwards through the following transparent structures—cornea, aqueous humour, crystalline lens, and vitreous humour. The *sclerotic* may be regarded as a strong fibrous tunic determining the form of the eyeball, and supporting the more delicate structures. The *cornea* is also a firm membrane; it is covered on the anterior surface by several layers of transparent pavement epithelium, reflected from the conjunctiva; the proper substance of the cornea is formed of a series of transparent laminæ, amongst which are numerous connective tissue corpuscles; and the posterior surface, next the aqueous humour, is lined by a homogenous elastic membrane, the membrane of Descemet, covered by one layer of epithelial cells.

The *choroidal layer* consists of connective tissue, permeated by numerous vessels, and lined in its internal surface by a layer of black pigment. Its anterior part forms a series of folds, termed the *ciliary processes*, which are richly supplied with capillaries. In the anterior part of the choroidal layer there are two contractile structures, the *ciliary muscle* and the *iris*. The first, arising from the convex surface of the choroid, is inserted into the transparent membrane forming the anterior part of the capsule of the lens. The *iris* is formed of a stroma of connective tissue, containing numerous bloodvessels, and having the posterior surface lined by pigment cells, and the anterior surface covered by an epithelial layer continuous with Descemet's membrane. Mixed with the stroma, there are two layers of involuntary muscular fibre: one set, radiating from the margin of the pupil towards the circumference, may be termed the *dilator* of the pupil; and the other set, forming a circular band, is known as the *constrictor* of the pupil. By contractions of these fibres, the pupil may become large or small.

The *vitreous humour* consists of a semi-fluid substance lying in a meshwork of connective tissue.

The *retina* is a transparent membrane during life, but after death it may become opalescent and of a bluish colour. Its posterior surface is applied to the choroid, and its anterior is separated from the vitreous humour by a thin transparent hyaloid membrane. In the fresh condition, when examined microscopically, it shows little trace of structure; but if it be hardened by alcohol or chromic acid, it may be cut into thin sections perpendicular to its surface. Its structure may also be elucidated by immersing the sections in staining solutions, or, still better, in solutions of osmic acid. In a successful section, the following layers, proceeding from the surface next the choroid, may be observed: (1) a layer, often termed *Jacob's membrane*, formed of remarkable structures, which, from their shape, are known as the *rods* and *cones;* (2) an external layer of granules of considerable size; (3) a middle layer of very minute granules; (4) an internal layer of granules; (5) a layer of ganglionic nerve-cells; and (6) a layer of nerve fibres, continuous with the optic nerve. It is probable that all of these layers are intimately connected together, and that each rod and each cone is in direct continuity with the termination of an optic nerve fibre. (See Fig. 139.)

It is important to observe that the apices of the rods and cones are directed towards the choroid, and that their other extremities point towards the interior of the eye. Before rays of light reach this layer, they must have traversed the other transparent layers of the retina—first the fibrous, derived from the optic nerve, and afterwards the granular layers.

As the rods and cones are the parts sensitive to light, it is necessary to notice the observations of Max Schultze regarding their minute structure, which will be understood with the aid of Fig. 139. Each rod and cone consists of two parts: an external—cylindrical, and similar in appearance in both rods and cones; and an internal—the form of which constitutes the chief difference between the two. In the cones, it is somewhat pyriform, and in the rods it is cylindrical. The external part is homogeneous and double refractive to light, whilst the other is usually finely granular, and exhibits a tendency both to longitudinal and to transverse cleavage. At the junction of the two, small very refractive particles may often be seen, and in many birds these are frequently of a red or yellow colour. In Fig. 139, the internal granulated layer of Max Schultze is marked 4, the inner granule layer 5, the external granulated layer 6, the external granule layer 7, and the layer of rods and cones 9.

It has been ascertained that cones abound in the retinæ of animals, such as nocturnal birds, which are

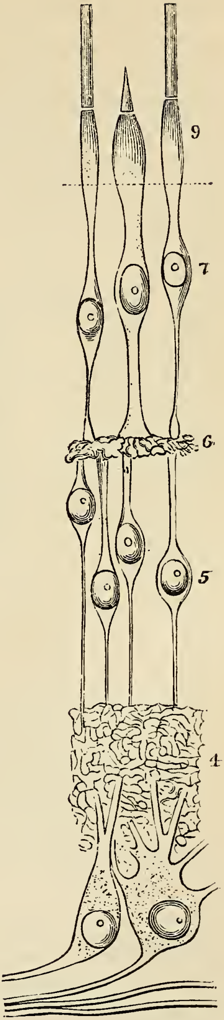


Fig. 139.—Elements of Retina according to Max Schultze.

sensitive to faint lights, and that in the yellow spot, which is the most sensitive part of the human eye, only cones exist. At the point of entrance of the optic nerve, in the centre of the retina, only the fibrous layer exists, and, as will be shown, this area is insensible to light. A few of the special histological characters of the rods and cones which must have an effect on retinal impressions is shown in Fig. 140.

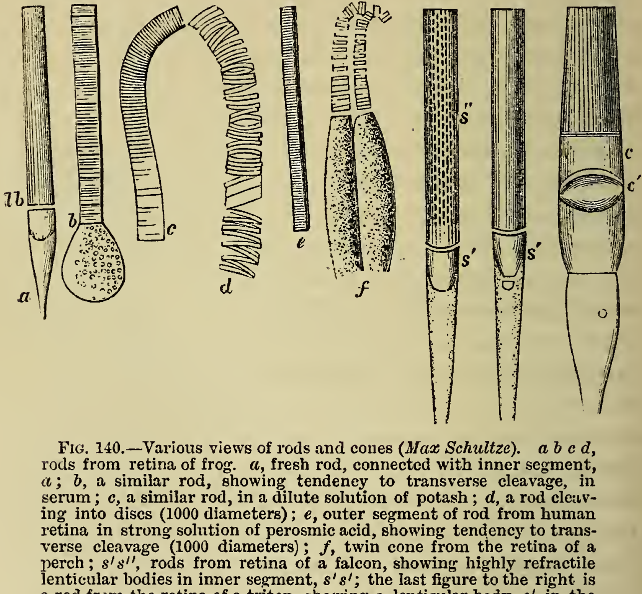


Fig. 140.—Various views of rods and cones (*Max Schultze*). *a b c d*, rods from retina of frog. *a*, fresh rod, connected with inner segment, *a*; *b*, a similar rod, showing tendency to transverse cleavage, in serum; *c*, a similar rod, in a dilute solution of potash; *d*, a rod cleaving into discs (1000 diameters); *e*, outer segment of rod from human retina in strong solution of perosmic acid, showing tendency to transverse cleavage (1000 diameters); *f*, twin cone from the retina of a perch; *s′s″*, rods from retina of a falcon, showing highly refractile lenticular bodies in inner segment, *s′s′*; the last figure to the right is a rod from the retina of a triton, showing a lenticular body, *c′*, in the internal segment.

The eyeball is moved in its socket by six muscles, and it is protected by the eyelids. In the latter, small glands, called the *meibomian glands*, secrete a fluid for lubricating the surface of the eye, which is also moistened by the secretion of the lachrymal gland.

2. PHYSICAL CAUSES OF VISION.

A luminous sensation may be caused by various kinds of irritation of the retina or of the optic nerve. Pressure, cutting, or electrical shocks may act as stimuli, but the normal stimulus is the action of light on the retina. Physically, light is a mode of motion, occurring in a medium, termed the ether, which pervades all space. When the movements of light act on the retina with sufficient intensity, molecular changes occur in that structure which in turn excite the fibres of the optic nerve; then a stimulus is conveyed to the brain, and the result is a sensation of light. Thus, light is regarded by the physicist as a mode of movement, or a condition of matter; whilst the physiologist studies the effect of these movements on the sentient organism. Such movements, acting on retina, optic nerve, and brain, result in consciousness of a particular kind which we call a luminous impression. Outside of the body, these movements have been studied with a great degree of accuracy and precision; but within the organism, as we have to deal with more complex conditions, it is impossible to follow them in the same way. We are conscious only of the result, say of red or of violet light; but the physicist states that in the first instance, the sensation of red, at the lower end of the spectrum, is produced by 435 billions of impulses per second, and that the sensation of violet, at the upper end, corresponds to 764 billions of impulses per second. Below the low red and above the high violet vibrations still occur, but they do not cause luminous sensations. The rays below the low red are thermal rays, whilst those beyond the extreme violet are distinguished by their chemical activity. Thus, we have thermal, luminous, and actinic rays, the intensities of which are represented graphically in the following figure.

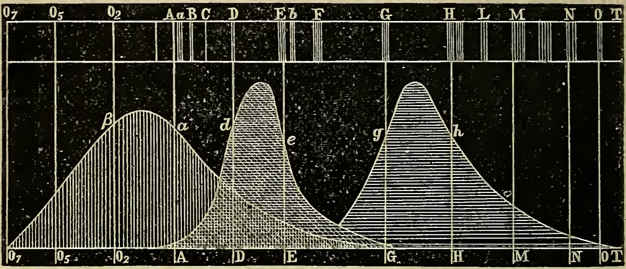


FIG. 141. - Curves of the intensity of thermal, luminous, and actinic rays in the different regions of the solar spectrum. The *luminous* spectrum ranges from A to G; the *ultra violet*, from G to T; and the *ultra red* from O_7 to A.

The number of vibrations of the extreme violet is not double that of the low red, so that the sensibility of the eye to vibrations of light does not range through an octave. The ultra-violet rays may act on the retina in certain conditions, as when they are reflected by a solution of sulphate of quinine, constituting the phenomenon of *fluorescence*. White light when passed through a prism is decomposed or dispersed so as to produce a spectrum.

When light traverses any homogeneous transparent medium, such as the air, it passes on in a straight course with a certain velocity; but if it meet with any other transparent body of a different density, part of it is reflected or returned to the first medium, whilst the remainder is propagated through the second medium in a different direction and with a different velocity. Thus we have the phenomena of reflexion and of refraction.[1] Let *a b* be a plane surface of some transparent substance, say a sheet of glass; a ray of

---

[1] The student ought to make himself familiar with the general laws of reflexion and of refraction, as given in any work on Natural Philosophy.

light, *c d*, perpendicular to the surface, will pass through without refraction; but an oblique ray, such as *e f*, will be bent in the direction *e h*. If the ray *e h* had passed from a dense into a rarer medium, then the direction would be *e g*. It can also be shown that the *sine* of the angle of incidence always bears a certain ratio to the *sine* of the angle of refraction, and this ratio is termed the *index of refraction*. Thus, if a ray passes from air into water, the sine of the angle of incidence will be to the sine of the angle of refraction as 4 : 3, or $\frac{4}{3}$. When a ray passes from a more refractive to a less refractive medium, the index of refraction is always greater than unity, and is represented in formulæ by n; in the reverse circumstances, the index of refraction is less than unity and is represented by $\frac{1}{n}$.

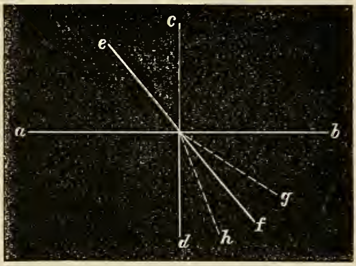


FIG. 142.—Diagram illustrating refraction of light.

3. THE OPTICAL ARRANGEMENTS OF THE EYE.

a. *The Optical Constants.*

A ray of light must pass through the following transparent structures before it reaches the retina: cornea, aqueous humour, anterior layer of the capsule of the lens, the lens itself, the posterior layer of its capsule, and the vitreous humour. As the two surfaces of the cornea are parallel, the rays suffer no deviation in passing through that structure; but they are refracted in passing through the other structures. To ascertain the exact course of the rays, it is necessary to know the radius of curvature of the refracting surface and the index of refraction. The radius of curvature of the anterior surface of the cornea is 8 mm.; that of the anterior surface of the lens, 10 mm.; and that of the posterior surface, 6 mm. The indices of refraction are: aqueous humour, $\frac{103}{77}$ = 1·3379; lens, $\frac{16}{11}$ = 1·4545; and vitreous humour, $\frac{103}{77}$ = 1·3379. Thus, the eye may be regarded as a centred dioptric system, formed of several refracting media. In such a system there are six cardinal points: (1) *Two focal points*, an anterior and a posterior, the properties of which are that all the rays starting from the anterior focal point proceed parallel to the axis, and all these parallel rays come to a focus at the posterior focal point; (2) *Two principal points*, through which pass *two principal planes*, representing the two surfaces of ideal separation of transparent media—every ray which passes through one point must pass through the other point, and every ray which passes through a point in the first principal plane must pass through a corresponding point in the second principal plane, at the same distance from the axis; (3) *Two nodal points*, which correspond to the optical centres of the two principal planes already alluded to. The term *anterior focal length* is given to the distance between the anterior focal point and the first principal point; and the term *posterior focal length* is applied to the distance of the posterior focal point to the second principal point. The positions, as measured in millimetres from the centre of the cornea,[1] of these cardinal points in the human eye have been determined as follows:—

	mm.		mm.
Anterior focal point,	12·8326	First nodal point,	7·2420
Posterior focal point,	22·6470	Second nodal point,	7·6398
First principal point,	2·1746	Anterior focal length,	15·0072
Second principal point,	2·5724	Posterior focal length,	20·0746

---

[1] These measurements are made chiefly with the aid of an instrument termed an opthalmometer, which is described in Appendix.

The positions of these cardinal points in a dioptric system, sometimes called the optical constants of Gauss, will be understood with the aid of the following diagram:—

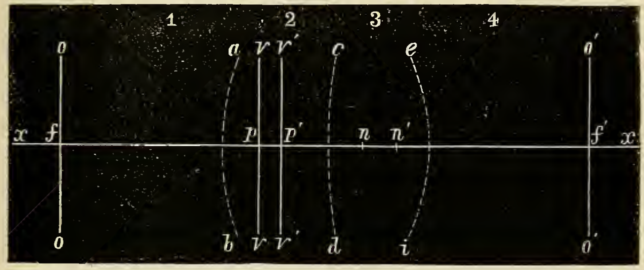


FIG. 143.—Centred dioptric system. *x x*, axis; 1, 2, 3, 4, four refractive media, separated by curved surfaces *a b*, *c d*, and *e i*; *f*, anterior focal point; *f′*, posterior focal point; *o o*, anterior focal plane; *o′ o′*, posterior focal plane; *p*, first principal point; *p′*, second principal point; *v v*, anterior principal plane; *v′ v′*, posterior principal plane; *n*, first nodal point; *n′*, second nodal point; *f p*, anterior focal length; *f′ p′*, posterior focal length.

b. *Formation of an Image on the Retina.*

The formation of an image upon the retina may be well illustrated with the aid of an ordinary photographic camera.

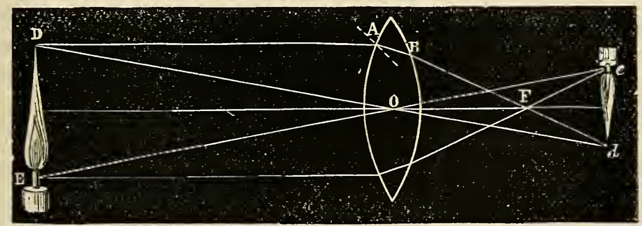


FIG. 144.—Inversion of an image by a bi-convex lens. D E, the object; F, posterior focal point of the lens, A B; inverted image, *e d*. Observe the crossing of certain of the rays at O, and of others at F. (*Wundt.*)

If properly focussed, an inverted image will be seen on the glass plate at the back of the camera. It may also be observed by bringing the eyeball of a rabbit near a candle, when a bright and inverted image may be seen even through the sclerotic. The action of a lens in forming an inverted image is shown in Fig. 144. An inverted image of a candle may also be formed without a lens by allowing the rays to enter a box through a narrow aperture, as shown in Fig. 145.

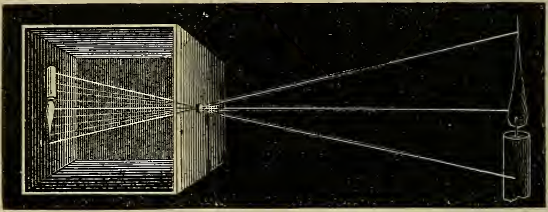


FIG. 145.—Arrangement for showing an inverted image. (*Wundt.*)

The three points to be kept in mind with regard to the retinal image are: (1) it is reversed; (2) it is sharp and well defined, if it be accurately focussed on the retina; and (3) its size depends on the visual angle. If we look at a distant object, say a star, the rays reaching the eye are parallel, and in passing through the refractive media, they are focussed at the posterior focal point, that is, on the retina. A line from the luminous point on the retina passing through the nodal point is called *the line of direction.* If the luminous object be not nearer than say 60 yards, the image is still brought to a focus on the retina without any effort on the part of the eye. Within this distance, supposing the condition of the eye to be the same as in looking at a star, the image would be formed somewhat behind the posterior focal point, and the effect would be an indistinct impression on the retina. To obviate this, for near distances, accommodation, so as to adapt the eye, is effected by a mechanism to be afterwards described.

The *inversion* of the image will be understood with the aid of Figs. 144 and 146. Suppose *c d e* to be luminous objects, the rays proceeding from their surface above the optic axis cross in the eye so as to be brought to a focus below the axis, and *vice versa*. Thus an inverted image is formed on the retina at *a b*. The angle x is termed the *visual angle*, and it is evident that its size will depend on the size of the object and the distance of the object from the eye. Thus, objects of different sizes, *c*, *d*, and *e*, may be included in the same visual angle, as they are at different distances from the eye. The *size* of the image on the retina may obviously be calculated if we know the size of the object, its distance from the nodal point *o*, and the distance of the nodal point from the posterior focus. Let A be the size of the object, B its distance from the nodal point, and C the distance of *o* from the retina = 15 millimetres: then the size of the retinal image, $X = \frac{A + 15}{B}$. The smallest visual angle in which two distinct points may be observed is 60 seconds; below this, the two sensations fuse into one; and the size of the retinal image corresponding to this angle is ·004 millimetres, nearly the diameter of a single retinal rod or cone. Thus, two objects included in a visual angle less than 60 seconds appear as one point.

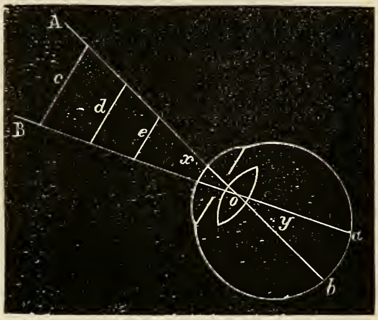


Fig. 146.—Diagram showing the visual angle.

A small visual angle is in most eyes a condition of sharpness of definition. With a large angle, objects appear less sharply marked. Acuteness is determined by a few or even only one retinal element being affected. A very minute image, if thrown on a single retinal element, is apparently sufficient to excite it. Thus, it is possible to see a brilliant point in an angle even so small as $\frac{1}{4}$ of a second, and a sharp eye can see a body the $\frac{1}{50}$th of a line in diameter—that is, about the $\frac{1}{600}$th part of an inch.

c. *Optical Defects of the Eye.*

As an optical instrument, the eye is defective; but from habit and want of attention its defects are not appreciated, and consequently they have little or no influence on our sensations. They are chiefly of two kinds: (1) those due to the curvature of the refractive surfaces; and (2) those due to the dispersion of light by the refractive media.

1. *Aberration of Sphericity.*—Suppose, as in Fig. 147, M A K to be a refractive surface on which parallel rays from L to S impinge, it will be seen that those rays passing near the circumference are brought to a focus at F^1, and those passing nearer the centre at F^2, intermediate rays being focussed at N. Thus, in the portion of the axis between

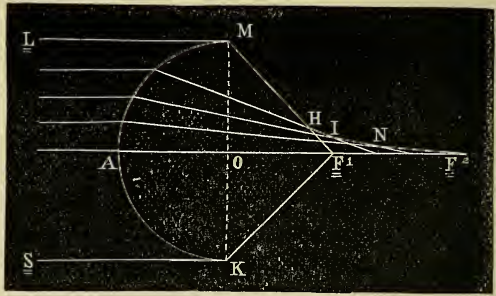


FIG. 147.—Diagram illustrating aberration of sphericity.

F^1 and F^2, there will be a series of focal points, and the effect will be a blurred and bent image. In the eye, this defect is to a large extent corrected by the following arrangements: (1) the iris cuts off the outer and more strongly refracted rays; (2) the curvature of the cornea is more ellipsoidal than spherical, and consequently those farthest from the axis are least deviated; (3) the anterior and posterior curvatures of the lens are such that the one corrects, to a certain extent, the action of the other; and (4) the structure of the lens is such that its power of refraction diminishes from the centre to the circumference, and consequently the rays farthest from the axis are less refracted.

Another defect of the eye is due to different meridians having different degrees of curvature. This defect is known as *Astigmatism*. It may be thus detected: draw with ink on a sheet of white paper a vertical and a horizontal line, crossing at a right angle; at the point of distinct vision, it will be found impossible to see the lines with equal distinctness at the same time; so that to see the horizontal line distinctly, the paper must be brought near the eye, and removed from it to see the vertical. In the cornea, the vertical meridian has a shorter radius of curvature, and is consequently more refractive than the horizontal. The meridians of the lens may also vary; but, as a rule, the asymmetry of the cornea is greater than that of the lens. The optical explanation of the defect will be understood with the aid of Fig. 148.

Thus, suppose the vertical meridian, C A D, to be more strongly curved than the horizontal, F A E, the rays which fall on C A D will be brought to a focus G; and those falling on F A E at B. If we divide the pencil of rays at successive points, G, H, I, K, B, by a section perpendicular to A B, the various forms it would present at these points are seen in the figures underneath; so that, if the eye were placed at

G, it would see a horizontal line *a a′*; if at H, an ellipse, with the long axis *a a′* parallel to A B; if at I, a circle; if at K, an ellipse, with the long axis *b c* at right angles to A B; and, if at B, a vertical line *b c*.[1] The degree of astigmatism is ascertained by measuring the difference of refraction in the two chief meridians; and the defect is corrected by the use of cylindrical glasses, the curvature of which, added to that of the minimum meridian, makes its focal length equal to that of the maximum meridian.

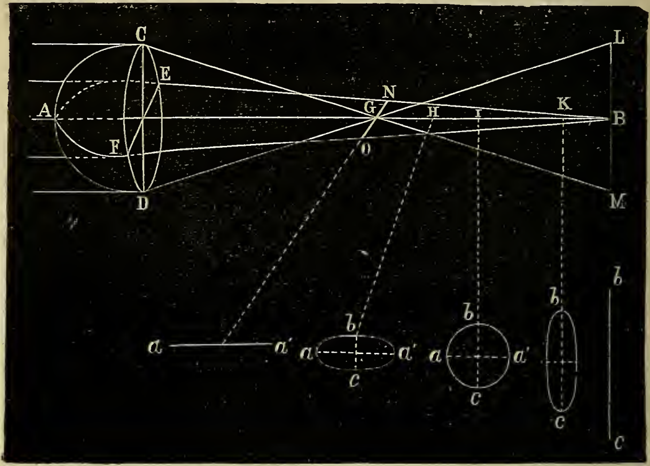


Fig. 148.—Diagram illustrating Astigmatism. See Text. (*Wundt.*)

(2) *Aberration of Refrangibility.*—When a ray of white light impinges on a lens, the different rays composing it, being unequally refrangible, are dispersed. The violet rays (see Fig. 149), the most refrangible, are brought into a focus

---

[1] An ingenious arrangement, consisting of threads of different colours, devised by Helmholtz, may be used to illustrate these facts.

at *e*; and the red rays, less refrangible, at *d*. If a screen were placed at *e*, a series of concentric coloured circles would be formed, the central being of a violet, and the circumference of a red, colour. The reverse effect would be produced if the screen were placed at *d*. Imagine the retina in place of the screen in the two positions; the sensational effects would be those just mentioned. Under ordinary circumstances, the error of refrangibility due to the optical construction of the eye, is not observed; as, for vision at near distances, the interval between the focal point of the red and violet rays is very small. If, however, we look at a candle flame through a bit of cobalt-blue glass, which transmits only the red and blue rays, the flame may appear violet surrounded by blue, or blue surrounded by violet, according as we have accommodated the eye for different distances. Red surfaces always appear nearer than violet surfaces situated in the same plane, because the eye has to be accommodated more for the red than for the violet, and consequently we imagine them to be nearer. Again, if we contemplate red letters or designs on a violet ground, the eye soon becomes fatigued, and the designs may appear to move.

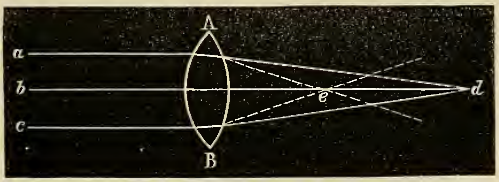


FIG. 149.—Diagram illustrating the dispersion of light by a lens.

(3) *Defects due to Opacities, &c., in the Transparent Media.*—When small opaque particles exist in the transparent media, they may cast their shadow on the retina, so as to give rise to images which are projected outwards by the mind into space, and thus appear to exist outside of the

body. Such phenomena are termed *entoptic*, and they may be of two kinds: (1) *extra-retinal*, that is, due to opaque or semi-transparent bodies in any of the refractive structures anterior to the retina, and presenting the appearance of drops, striæ, lines, twisted bodies, forms of grotesque shape, or minute black dots dancing before the eye; and (2) *intra-retinal*, due to opacities, &c., in the layers of the retina in front of Jacob's membrane. The intra-retinal phenomena may be produced, in a normal eye, in various ways: (1) Throw a strong beam of light on the edge of the sclerotic on the outer part of the eye, and a curious branched figure will be seen, which is an image of the retinal vessels. (*Purkinje's figures*); (2) Look at a strong light through a minute aperture, in front of which a rapid to-and-fro movement is made, and an image of the vessels will also be seen; and (3) Look at a very brilliant light passing through a long tube, moving the head to and fro, and numerous round and faintly-marked bodies, the blood-corpuscles, may be detected. Thus, by such arrangements, an observer may see the circulation in his own eye. Such experiments also prove that the sensitive part of the retina is its deepest and most external layer. (Jacob's membrane).

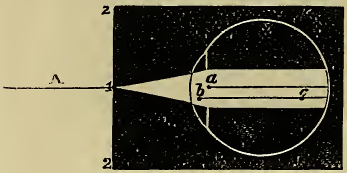


FIG. 150—Diagram illustrating entoptic phenomena. 2 2, a screen, admitting light from A, by a minute aperture 1. Observe the form of the pencil of rays. *a b*, minute bodies (extra-retinal) casting a shadow on retina; *c*, body (intra-retinal), casting a shadow on Jacob's membrane.

d. *Accommodation or the Mechanism of Adjustment for different distances.*

When a camera is placed in front of an object, it is necessary to focus accurately in order to obtain a clear and distinct image on the sensitive plate. This may be done by moving either the lens or the sensitive plate backwards or forwards, so as to have the posterior focal point of the lens corresponding with the sensitive plate. For similar reasons, a mechanism of adjustment, or accommodation for different distances, is necessary in the human eye. In the normal eye any number of parallel rays, coming from a great distance, are focussed on the retina. Such an eye is termed *Emmetropic* (Fig. 151, A). Another form of eye (B) may be such that parallel rays are brought to a focus in *front* of the retina. This form of eye is *myopic* or short-sighted, inasmuch as for distinct vision, the object must be brought near the eye, so as to catch the divergent rays which are then focussed on the retina. A third form is seen in C, where the focal point, for ordinary distances, is *behind* the retina, and consequently the object must be held far off, so as to allow only the less divergent or parallel rays to reach the eye. This kind of eye is called *Hypermetropic* or far-sighted. For ordinary distances at which objects must be seen distinctly in every-day life, it is evident the fault of the myopic eye may be corrected by the use of concave, and of the hypermetropic, of convex, glasses. In the first case, the con-

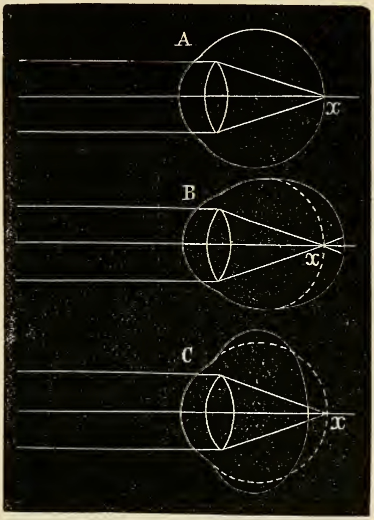


FIG. 151.—A, Emmetropic or normal eye; B, Myopic or short-sighted eye; C, Hypermetropic or long-sighted eye.

cave glass will remove the posterior focal point a little farther back, and in the second, the convex glass will bring it farther forwards; in both cases, however, the glasses may be so adjusted, both as regards refractive index and radius of curvature, as to bring the rays to a focus on the retina, and consequently secure distinct vision.

From any point sixty-five metres distant, rays may be regarded as almost parallel, and the point will be seen without any effort of accommodation. This point, either at this distance or in infinity, is called the *punctum remotum*, or the most distant point seen without accommodation. In the myopic eye it is much nearer, and for the hypermetropic, there is really no such point, and accommodation is always necessary.

In the normal eye, as already stated, parallel rays coming from infinity are brought to a focus on the retina. When the rays are not brought accurately to a focus on the retina, the image is indistinct, and *circles of diffusion* are formed. These may be readily studied by the following experiment, known as the *Experiment of Scheiner*.

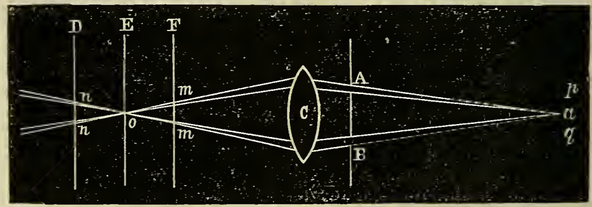


FIG. 152.—Experiment of Scheiner.

Let C be a lens, and D E F be screens placed behind it; hold in front of the lens a card perforated by two holes A and B, and allow rays from a luminous point *a* to pass through these holes; the point *o* on the screen E will be the exact focus of the rays emanating from *a*; if *a* were removed farther from the lens, the focus would be on F, and if it were brought nearer to C, the focus would then be on D. The screens F and D show two images of the point *a*. If then we close the upper opening in A B, the *upper* image *m* on F and the *lower* image *n* on the screen D, disappears. Suppose then that the retina be substituted for the screens D and F, the contrary will take place in consequence of the reversal of the retinal image. If the eye be placed at *o*, only one image will be seen, but if it be placed either in the plane of F or D, then two images will be seen as at *m m* or *n n*, consequently in either of these planes there will be circles of diffusion and indistinctness, and only in the plane E will there be sharp definition of the image.

From the above considerations, it is evident that if an object be brought too close to the eye for the refractive media to focus it on the retina, circles of diffusion will be formed, with the result of causing indistinctness of vision, unless the eye possess some power of adapting itself to different distances. That the eye has some such power of accommodation is proved by the fact that if we attempt to look through the meshes of a net at a distant object, we cannot see both the meshes and the object with equal distinctness at the same time. Again, if we look continually at very near objects, the eye speedily becomes fatigued. Beyond a distance of sixty-five metres, no accommodation is necessary, but within it the condition of the eye must be adapted to the diminished distance until we reach a point near the eye, which may be regarded as the limit of visibility for near objects. This point, called the *punctum proximum,* is usually twelve centimetres from the eye. The range of accommodation is thus from the punctum remotum to the punctum proximum.

The mechanism of accommodation has been much disputed, but there can be no doubt it is chiefly effected by a change in the curvature of the anterior surface of the crystalline lens. If we hold a lighted candle in front, and a little to the side, of an eye to be examined, three reflections may be seen in the eye. This experiment may be done with considerable facility by using an instrument devised by Helmholtz, and termed a *Phakoscope*, shown in Fig. 153. It consists of a triangular box having the three angles squared off as seen in the figure. To the left of the figure two prisms are seen, by which light from a candle is concentrated on the eye under examination. This eye is placed before an aperture on the side of the box opposite to *c*, and the eye of the observer is placed at *a*. The three images thus seen are shown in Fig. 154. The first, *a*, is erect, large and bright, from the anterior surface of the cornea; the second, *b*, also erect, but dim, from the anterior surface of the crystalline lens; and the third, *c*, inverted, and very dim, from the posterior surface of the lens, or perhaps the concave surface of the vitreous humour to which the convex surface of the lens is adapted. Suppose the individual gazes at a distant object through the window *c*, and the relative position of the images be noted, if he then be directed to fix his eye on a needle point, suddenly pushed up by the shutter *c*, the observer at *a* will see the image *b* (in

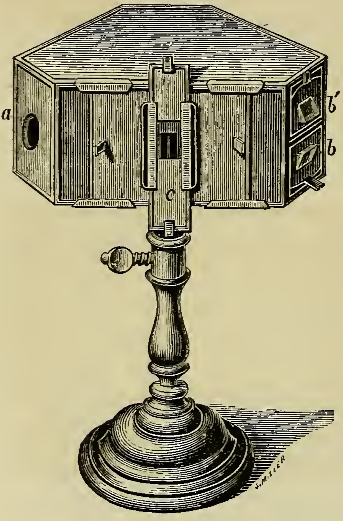


FIG. 153.—Phakoscope of Helmholtz. For description, see text.

Fig. 154) advance towards *a*, that is the anterior surface of the lens becomes more convex. The change in convexity is shown in Fig. 155. The changes occurring during accommodation are: (1) the curvature of the anterior surface of the crystalline lens increases, and may pass from ten to six millimetres; (2) the pupil contracts; and (3) the intra-ocular pressure increases in the posterior part of the eye. An explanation of the increased curvature of the anterior surface of the lens during accommodation has been thus given by Helmholtz. In the normal condition, that is for the emmetropic eye, the crystalline lens is flattened anteriorly by the pressure of the anterior layer of the capsule; during accommodation, the radiating fibres of the ciliary muscle pull on the capsule so as to relieve its tension, and the lens at once bulges forward by its elasticity.[1]

Fig. 154.—Reflected images in the eye.

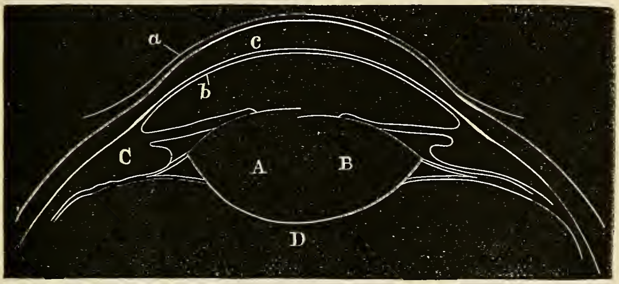


Fig. 155.—Mechanism of accommodation. A, the lens during accommodation showing its anterior surface advanced; B, the lens as in distant vision; C, position of the ciliary muscle; D, the vitreous; *a*, anterior elastic lamina of cornea; *c*, corneal substance proper; *b*, posterior elastic lamina, or membrane of Descemet.

---

[1] We are indebted largely to Helmholtz for our present theory of the Mechanism of Accommodation, and for the means of making

d. *Absorption and Reflection of Luminous Rays from the Eye.*

When light enters the eye, it is partly absorbed by the black pigment of the choroid and partly reflected. The reflected rays are returned through the pupil, following not only the same direction as the rays entering the eye, but uniting to form an image at the same point in space as the luminous object. The pupil of an eye appears black to an observer, because the eye of the observer does not receive any of these reflected rays. If, however, we strongly illuminate the retina, and hold a lens in front of the eye to be observed, so as to bring these reflected rays to a focus on the retina of the observing eye, then an image of the retina will be seen. Such is the principle of the *ophthalmoscope*, invented by Helmholtz in 1851.

Eyes deficient in pigment, as in albinos, appear luminous, reflecting light of a red or pink colour; but if we place in front of such an eye a card perforated by a round hole of the diameter of the pupil, the hole will appear quite dark, like the pupil of the ordinary eye. In many animals, a portion of the fundus of the eyeball has no pigment, and presents an iridescent appearance. This is called a *tapetum*, and probably renders the eye more sensitive to light of feeble intensity.

---

accurate measurements. This he accomplished by using an instrument invented by himself termed an *ophthalmometer*, by which the sizes of the reflected images can be measured with accuracy. Thus he ascertained that during accommodation the mid reflected image becomes smaller, in consequence of the anterior surface of the lens becoming more convex; and from the data thus supplied, he calculated the radius of curvature. A description of the apparatus and of the mode of using it was written by the author for Bennett's Text-Book of Physiology, p. 563. It will be found in Appendix E.

c. *Functions of the Iris.*

The iris constitutes a diaphragm which regulates the amount of light entering the eyeball. The aperture in the centre, the *pupil*, may be dilated by contraction of a system of radiating fibres of involuntary muscle, or contracted by the action of another system of fibres forming a sphincter at the margin of the pupil. The radiating fibres are controlled by the sympathetic, while those of the circular set are excited by the third cranial, nerve. The variations in diameter of the pupil are determined by the greater or less intensity of the light acting on the retina. A strong light causes contraction of the pupil; with light of less intensity, the pupil will dilate. In the human being, a strong light acting on one eye will often cause contraction of the pupil not only in the eye affected but in the other eye. These facts indicate that the phenomenon is of the nature of a reflex action, in which the fibres of the optic nerve act as sensory conductors to a centre in the encephalon whence influences emanate which act on the pupil. It has been ascertained, that if the fibres of the optic nerve be affected in any way, contraction of the pupil follows. The centre is probably in the anterior pair of the corpora quadrigemina, as destruction of these bodies causes immobility of the pupil. On the other hand, the dilating fibres are derived from the sympathetic; and it has been shown that they come from the lower part of the cervical, and upper part of the dorsal, region of the cord. But the iris seems to be directly susceptible to the action of light. Thus, as was first pointed out by Brown-Séquard, the pupil of the eye of a dead animal will contract if exposed to light for several hours, whereas, if the eye on the opposite side be covered, its pupil will remain widely dilated, as at the moment of death. This phenomenon is seen with most marked effect in the eyes of cats.

The pupil *contracts* under the influence: (1) of an increased intensity of light; (2) of the effort of accommodation for near objects; (3) of a strong convergence of the two eyes; and (4) of such active substances as nicotine, morphia, and physostigmine; and it *dilates* under the influence: (1) of a diminished intensity of light; (2) of vision of distant objects; (3) of a strong excitation of any sensory nerve; (4) of dyspnœa; and (5) of such substances as atropine and hyoscyamine. The chief function of the iris is so to moderate the amount of light entering the eye as to secure sharpness of definition of the retinal image. This it accomplishes by (1) diminishing the amount of light reflected from near objects by cutting off the more divergent rays and admitting only those approaching a parallel direction, which, in a normal eye, are focussed on the retina; and (2) preventing the error of chromatic aberration by cutting off divergent rays which would otherwise impinge near the margin of the lens, and would thus be brought to a focus in front of the retina.

4. Normal Excitation of the Retina.

The retina is the terminal organ of vision, and all the parts in front of it are merely optical arrangements for securing that an image will be accurately focussed upon it. The natural stimulus of the retina is light. It is often said that it may be excited by mechanical and electrical stimuli; but such an observation really applies to the stimulation of the fibres of the optic nerve. It is well known that such stimuli applied to the optic nerve behind the eye produce always a luminous impression; but there is no proof that the retina, strictly speaking, is similarly affected. Pressure or electrical currents may act on the eyeball, but in doing so they not only affect the retina, consisting of its various layers and of Jacob's membrane, but also the fibres of the optic nerve. It is probable that the retina, by which the author means all the layers except those on its surface formed by the fibres of the optic nerve, is affected only by its *specific* kind of stimulus, light. This stimulus so affects the terminal apparatus as to set up actions which in turn stimulate the optic fibres. The next question naturally is—What is the specific action of light on the retina? Professor

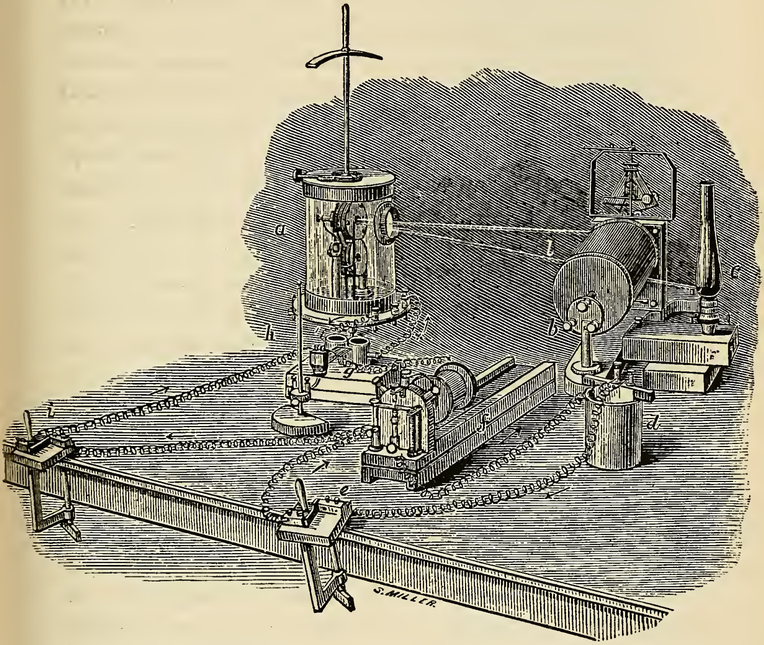


FIG. 156.—Arrangement of apparatus for obtaining a graphic tracing of the movement of a galvanometer, in various physiological experiments. *a*, galvanometer, by the mirror of which the ray, *l*, is reflected on the cylinder, *b*, from the lamp, *c*; *g*, troughs in connection with galvanometer, the key, *i*, being interposed. The induction coil, *f*, worked by cell *d*, and key *e*, may be used in other experiments for stimulating any preparation placed in the troughs, *g*.

Holmgren, of Upsala, individually, and Professor Dewar and the author conjointly, have shown that when light falls on the retina it excites a variation of the natural electrical current, obtained from the eye by placing it on the cushions of a sensitive galvanometer. (See p. 105.) To register such a variation, the arrangement shown in Fig. 156 is very convenient. The eye is placed on the clay pads of the troughs, the one pad touching the cornea and the other the posterior part of the eyeball. When the key is opened, there is a swing of the needle of the galvanometer, and the spot of reflected light, after taking up a position and remaining tolerably steady, may be brought to the centre of the surface of the revolving cylinder, and in the dark, it would mark the dotted line *a h*, seen in Fig. 157. If light be thrown on the eye at *a*, the needle of the galvanometer swings to the right, as indicated by the curve *a b c*, indicating *an increase in the natural current;* during the action of light, the current falls below the normal amount, as shown by the curve *c d e;* and on the removal of light, as at *e*, there is often a second increase of the current, as shown by the curve *e f g;* afterwards the amount of current falls below the normal. These results were ascertained by experiments on many eyes of different animals, and they show that light produces a variation of the natural electrical current obtained from the living eye. It was also ascertained in this research that the amount of electrical variation produced by light of various intensities corresponded pretty closely to the results expressed in Fechner's law, as stated on page 544. If so, then this law applies to the phenomena happening in the terminal organ, and not, as generally supposed, *only* to those occurring in the brain. Such electrical phenomena would probably result either from thermal or chemical changes in the retina. Recent researches of Boll and Kühne have shown that light produces chemical changes in the retina.

If an animal be killed in the dark, and its retina be exposed only to *yellow* rays, the retina has a peculiar purple colour, which is at once destroyed if exposed to ordinary light. The purple matter is decomposed by light. Kühne has also shown that an image may actually be *fixed* on the retina by plunging it into a solution of alum, immediately after death. Thus it would appear that light affects the purple matter of the retina, and the result of this chemical change is to stimulate the optic filaments; if the action be arrested, we may have a picture on the retina; but if it be not arrested, the picture is evanescent—the purple matter is used up, and new matter, of the same kind, is formed to take its place. The retina might, therefore, be compared to a sensitive plate having the sensitive matter quickly removed and replaced, by chemical changes; and it is probable that the electrical expression of these changes is what has been above described.

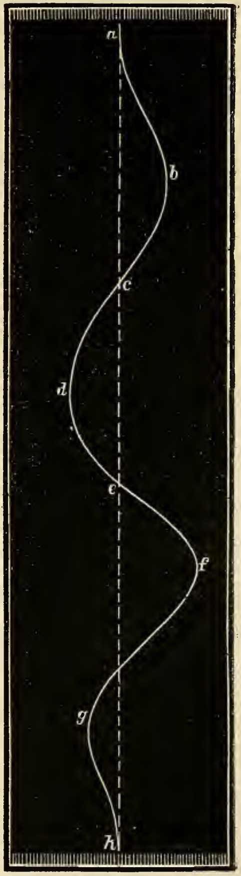


FIG. 157.—Curve of the variation in the natural electrical current of the eye produced by the action of light.

Luminous impressions may also be produced by pressure on the eyeball. Such impressions, termed *phosgenes,* usually appear as a luminous centre, surrounded by coloured or dark rings.

Sometimes they seem to be small, bright scintillations of various forms. Similar appearances may be observed at the moment of opening or of closing a strong electrical current transmitted through the eye-ball.

The visual field, even when the eyelids are closed, in a dark room, is not absolutely dark. There is a sensation of faint luminosity, which may at one moment be brighter than at another. This is often termed *the proper light of the retina*, and it indicates a certain condition of molecular activity, even in darkness.

a. *The Excitability of the Retina.*

The retina is not equally excitable in all its parts. At the entrance of the optic nerve, as was shown by Mariotte in 1668, there is no sensibility to light; hence this part of the retina is called the *blind spot*. If we shut the left eye, fix the right eye on the cross seen in Fig. 158, and move the book towards and from the eye, a position will be found when the round spot disappears, that is, when its image falls on the entrance of the optic nerve. There is also complete insensibility to colours at that spot. The diameter of the optic papilla is about 1·8 mm.; this gives an angle of six degrees; this angle determines the apparent size of the blind

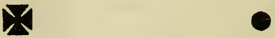


Fig. 158.

spot in the visual field, and it is sufficiently large to cause a human figure to disappear at a distance of two metres.

The *yellow spot* in the centre of the retina is the most sensitive to light; and it is chiefly employed in direct vision. Thus, if we fix the eye on a word in the centre of this line, it is distinctly and sharply seen, but the words towards each end of the line are vague. If we wish to see each word distinctly, we "run the eye" along the line—that is, we bring each successive word on the yellow spot. This spot has a horizontal diameter of 2 mm., and a vertical diameter of ·8 mm.; and it corresponds in the visual field to an angle of from two to four degrees. It is believed that the fossa in the spot, where there are almost no retinal elements except Jacob's membrane, consisting here entirely of cones (2,000 in number), is the area of most acute sensibility. This fossa has a diameter of only ·2 mm., which makes the angle ten times smaller. Thus the field of distinct vision is extremely limited; and, at the same moment, we see only a very small portion of the visual field. Images of external objects are brought successively on this minute sensitive area, and the different sensations seem to be fused together, so that we are conscious of the object as a whole.

Towards the anterior margin of the retina, sensitiveness to light becomes diminished; but the diminution is not uniform, and it varies in different persons.

b. *Duration and Persistence of Retinal Impressions.*

To excite the retina, a feeble stimulus must act for a certain time; but, if the stimulus be strong, it may be of very short duration. When the retina is excited, the impression lasts after the cessation of the stimulus. Thus the duration of an electrical spark is of extremely short duration, but the impression on the retina is so powerful, and remains so long, as to make the spark visible. If we rotate a disc having white and black sectors, we see continuous dark bands. Even if we paint on the face of the disc a single large, round, red *spot*, and rotate it rapidly, a continuous red *band* may be observed. Here the impressions of red on the same area of retina succeed each other so rapidly that before one disappears another is superadded; the result being a fusion of the successive impressions into one continuous sensation. This phenomenon is called the persistence of retinal impressions. It has been ascertained that an impression lasts on the retina from the $\frac{1}{50}$th to $\frac{1}{30}$th of a second. If we look steadily at a bright light for a few seconds, and then

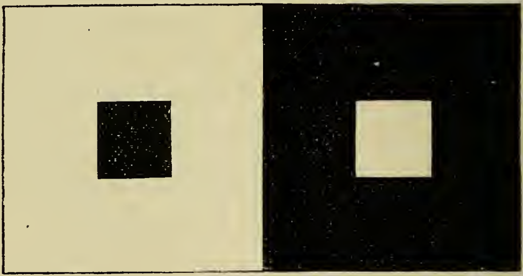


Fig. 159.—Illustration of Irradiation.

quickly close the eyes or gaze into a dark room, a luminous image of the light will be visible for a short time. Such an appearance is called a *positive accidental image*, or a consecutive image. It may also be observed in this experiment that the intensity of the retinal excitation is not uniform. It increases quickly at its commencement; and, after it has reached a maximum, it slowly declines; indeed, its progress might be represented graphically by the muscle curve (Fig. 21, p. 119). Many familiar toys, such as the thaumatrope, or wheel of life, stroboscopic discs, and the phénakistoscope, produce curious effects due to persistence of retinal impressions.

If we look at Fig. 159, the white square in the black field appears to be larger than the black square in the white field, though both are of precisely the same size. This is due to *irradiation*, a phenomenon explained by Helmholtz by stating that the borders of the clear surfaces advance in the visual field, and encroach on obscure surfaces. It is probable that even with the most exact accommodation, a penumbra or shadow of diffusion images forms around the edge of a white surface, so as to cause it to appear larger than it really is.

c. *Intensity of Light required to Excite the Retina.*

To excite the retina, light must have a certain intensity. It is impossible to fix the minimum intensity necessary, as the effect will depend not only on the intensity of the stimulus, but on the degree of retinal excitability at the time. Thus, after the retina has been for some time in the dark, its excitability is increased; on the other hand, it is much diminished by fatigue. The sensibility of the eye to light is measured by instruments termed *photometers;* the principle of which is that the intensities of two lights are inversely proportional to the squares of their distance from a screen.

d. *Consecutive Retinal Images.*

Images which persist on the retina are either positive or negative. They are termed *positive* when the bright and obscure parts of the image are the same as the bright and obscure parts of the object; *negative* when the bright parts of the object are dark in the image, and *vice versa.* Positive images are strong and sharply marked when an intense light has acted for not less than the one-third of a second. If the excitation be continued much longer, a negative, and not

Fig. 160.—Figure to illustrate the formation of a consecutive image. (Spectropia.)

a positive image, will be seen. If, when the positive image is still visible, we look on a very brilliantly illuminated surface, a negative image appears. Negative images are seen with greatest intensity after a strong light has acted for a considerable time. These phenomena may be best studied when the retina is very excitable, as in the morning, after a sound sleep. On awaking, if we look steadily *for an instant* at the window, and then close the eyes, a *positive* image of the window will appear; if we then gaze fixedly at the window for one or two minutes, then close the eyes two or three times, and then look at a dark part of the room, a *negative* image will be seen floating before us. The positive image is due to excitation of the retina, and the negative to fatigue. If we fatigue a small area of the retina with white light, and then allow a less intense light to fall on it, the fatigued area responds feebly, and consequently, the object, such as a window pane, appears to be dark. Many curious experiments may be made to illustrate the laws of consecutive images.

Thus, if we stand near a gaslight and look fixedly, without winking, at the little black dot under the chin of the figure seen in Fig. 160, for one minute, and then, after closing the eyelids two or three times, if we gaze into a dark part of the room, a white spectre will be seen floating in the air before us. A similar figure, white on a black ground, will produce a black spectre; a green figure will produce a red; a red, a green; the reproduced colour being always complementary to that of the figure. No doubt, many spectral illusions, which were accepted as true by the superstitious, have been produced in some such way.

5. Sensations of Colour.

Colour is a special sensation excited by the action on the retina of rays of light of a definite wave-length. Thus we have a sensation of red when a certain number of waves of light impinge on the retina in a unit of time, and with about twice the number of waves in the same time, the sensation will not be of red but of violet. When we examine a spectrum, we see a series of colours merging by insensible gradations the one into the other, thus: red, orange, yellow, green, blue, and violet. These are termed *simple* colours. If two or more coloured rays of the spectrum act simultaneously on the same spot of the retina, they may give rise to sensations of *mixed colours.* These mixed colours are of two kinds: (1) those which do not correspond to any colour in the spectrum, such as purple and white, and (2) those which do exist in the spectrum. White may be produced by a mixture of two simple colours, which are then said to be *complementary.* Thus red and greenish blue, orange and cyanic blue, yellow and indigo-blue, and greenish yellow and violet all produce white. Purple is produced by a mixture of red and violet or red and bluish violet. When white light falls on a surface, the surface may absorb all the rays except the red. If the red rays are alone reflected, then the object will be red; if the green rays are reflected, then the object will appear to be green. Again, if we look through a red glass, all the rays are absorbed except red, and consequently the world beyond appears to be red; so with regard to other transparent coloured media. The phenomena of colour may be readily studied by various methods; one of the simplest is that devised by Lambert, illustrated by Fig. 161, and it can be easily carried out by any student.

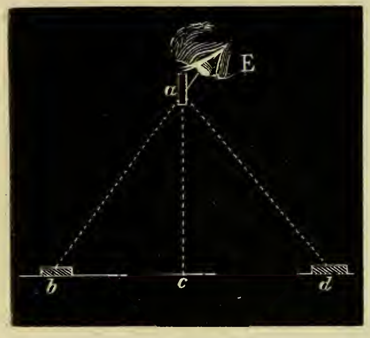


Fig. 161.—Lambert's method of studying combinations of colours.

Get a box of wafers of various colours, and a glass plate about four inches square, *a* in Fig. 161. Place a red wafer on *d* and a blue wafer on *b*, and so angle the glass plate as to throw a reflection of the object on *d in the same line* as the object on *b*. The sensation will then be purple. By substituting wafers of different colours, many experiments may thus be performed.

Another method is to use a rotating disc, on the surface of which coloured sectors are painted, as represented in Fig. 162. With sectors of the size seen in the figure, *white* will be produced on rotating the disc rapidly. This method has been carried out with great efficiency by the colour top of Clerk-Maxwell. It is simply a flat top, on the surface of which discs of various colours may be placed. Dancer has added to it a method by which even while the top is rotating rapidly, and the sensation of a mixed colour is strongly perceived, the eye may be able to see the *simple* colours of which it is composed. This is done by placing on the handle of the top, a short distance above the coloured surfaces, a thin black disc, perforated by holes of various size and pattern, and weighted a little on one side. This disc vibrates too and fro rapidly, breaks the continuity of the colour-impressions, and thus the constituent colours are readily seen.

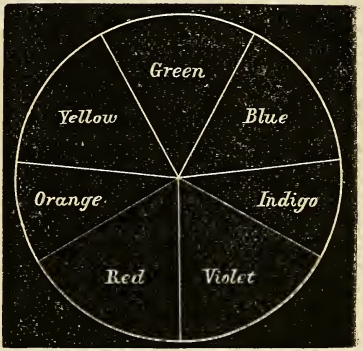


FIG. 162.—Rotating disc of Sir Isaac Newton for mixing colours.

All colours have three special characters: (1) *tone*, depending on the number of vibrations per second; (2) *intensity*, depending on the extent or amplitude of the vibrations, and passing from the most sombre to the most brilliant shades; and (3) *saturation*, which depends on the amount of *white* the colour contains—thus it is saturated, when there is no white, as in the pure colours of the spectrum, and there may be an infinite number of degrees of saturation from the pure colour to white.

a. *The Theory of Colour Perception.*

The theory generally accepted was first proposed by Thomas Young, and afterwards revived by Helmholtz. It is based on the assumption that three kinds of nerve fibres exist in the retina, the excitation of which give respectively sensations of red, green, and violet. These may be regarded as fundamental sensations. Homogeneous light excites all three, but with different intensities according to the length of the wave. Thus long waves will excite most strongly fibres sensitive to red, medium waves those sensitive to green, and short waves those sensitive to violet. Fig. 163 shows graphically the irritability of the three sets of fibres.

Helmholtz thus applies the theory:—

"1. Red excites strongly the fibres sensitive to red, and feebly the other two — sensation, *red.*
2. Yellow excites moderately the fibres sensitive to red and green, feebly the violet — sensation, *yellow.*
3. Green excites strongly the green, feebly the other two — sensation, *green.*
4. Blue excites moderately the fibres sensitive to green and violet, and feebly the red — sensation, *blue.*
5. Violet excites strongly the fibres sensitive to violet, and feebly the other two — sensation, *violet.*
6. When the excitation is nearly equal for the three kinds of fibres, then the sensation is *white.*"

This theory explains some of the phenomena of what is called *colour blindness* or *daltonism.* All individuals appear to have some kind of colour-sensation; in some, however, there may be no sensation for particular colours. The most common defect is insensibility to *red* (daltonism properly so called). The spectrum to such an eye is deficient in red, and the sensation corresponding to all compound colours containing red, is that of the complementary colour only. Thus white is bluish-green, and intense red appears green, so that red poppies in a green corn-field do not appear of a different hue from the green by which they are surrounded. If we suppose in such cases an absence or paralysis of the red fibres, the phenomena are accounted for. Blindness to green and violet are rare.

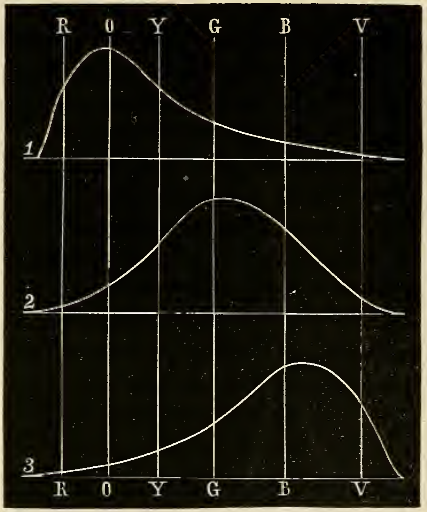


FIG. 163.—Diagram showing the irritability of the three kinds of retinal elements. 1 red, 2 green, 3 violet. R O Y G B V, initial letters of colours.

Young's theory also explains the appearance of the consecutive coloured images already referred to in p. 591. Suppose, for example, that we look at a red object for a considerable time, the retinal elements sensitive to red become fatigued. Then (1) if the eye be kept in *darkness,* the fibres affected by red being fatigued, do not act so as to give a sensation of red; those of green and of violet have been less excited, and this excitation is sufficient to give the sensation of pale greenish blue; (2) if the eye be fixed on a *white* surface, the red fibres being fatigued, are not excited by the red rays contained in the white light; on the contrary, the green and violet fibres are strongly excited, and the consequence is that we have an intense complementary image; (3) if we look at a *bluish green* surface, the complementary of red, the effect will be to excite still more strongly the green and violet fibres, and consequently to have a still more intense complementary image; (4) if we regard a *red* surface, the primitive colour, the red fibres are little affected, in consequence of being fatigued; the green and violet fibres will be only feebly excited, and therefore only a very feeble complementary image will be seen; and, (5) if we look at a surface of a *different* colour altogether, this colour may combine with that of the consecutive image, and produce a mixed colour, thus on a *yellow* surface we will see an image of an orange colour.

b. *The Contrast of Colours.*

If we look at a small white, grey, or black object on a coloured ground, the object appears to have the colour complementary to the ground. Thus, a circle of grey paper on a red ground appears to be of a greenish-blue colour, whilst on a blue ground it will appear pink. This effect is heightened, if we place over the paper a thin sheet of tissue paper; but it disappears at once if we place a black ring or border round the grey paper. Again, if we place two complementary colours side by side, both appear to be increased in intensity. Various theories have been advanced to explain these facts. Helmholtz is of opinion that the phenomena consist more in modifications in judgment than in modifications of sensation. Plateau, on the other hand, attempts to explain them by the theory of consecutive images.

6. Movements of the Eye.

The globe of the eye has a *centre of rotation* which is not exactly in the centre of the optic axis, but a little behind it. On this centre it may move round *axes of rotation*, of which there are three: an antero-posterior, a vertical, and a transverse. In normal vision, the two eyes are always placed in such a manner as to be fixed on one point, called the *fixed point*, or the *point of regard.* A line passing from the centre of rotation to the point of regard is called the *line of regard.* The two lines of regard form an angle at the point of regard, and the base is formed by a line passing from the one centre of rotation to the other. A plane passing through both lines of regard is called the *plane of regard.* With these definitions, we can now describe the movements of the eyeball, which are of three kinds: (1) *First Position.* The head is erect, and the line of regard is directed towards the distant horizon. (2) *Second Position.* This includes all the movements round the transverse and horizontal axes. When the eye rotates round the first, the line of regard is displaced above or below, and makes, with a line indicating its former position, an angle, termed by Helmholtz the angle of vertical displacement, or the *ascensional angle;* and when it rotates round the vertical axis, the line of regard is displaced from side to side, forming, with the median plane of the eye, an angle called the angle of lateral displacement. (3) *Third order of Positions.* This includes all those which the globe may assume in performing a rotatory movement, along with lateral or vertical displacements. This movement of rotation is measured by the angle which the plane of regard makes with the transverse plane, an angle termed the *angle of rotation* or of *torsion.* Listing has formulated the following law regarding the rotations of the eyeball: When the line of regard passes from its first position to any other position, the angle of torsion in this second position is the same as if the eye had come into this position in turning around a fixed axis perpendicular to the first and to the second position of the line of regard (*Helmholtz*). The result of this is that the axis of rotation of the eye is always in the frontal plane or equator of the eye. These facts may be readily studied by transfixing an orange with straight wires in the directions of the different axes, and attaching coloured threads to represent the lines of regard, &c.

The two eyes move together as a system, so that we direct the two lines of regard to the same point in space.

The eyeball is moved by six muscles, for a description of which reference is made to anatomical works. The following table summarizes their actions (*Beaunis*) :—

Number of Muscles in Activity.	Direction of Line of Regard.	Muscles Acting.
One,	Inwards,	Internal Rectus.
	Outwards,	External Rectus.
Two,	Upwards,	Superior Rectus. Inferior Oblique.
	Downwards,	Inferior Rectus. Superior Oblique.
Three,	Inwards and Upwards,	Internal Rectus. Superior Rectus. Inferior Oblique.
	Inwards and Downwards,	Internal Rectus. Inferior Rectus. Superior Oblique.
	Outwards and Upwards,	External Rectus. Superior Rectus. Inferior Oblique.
	Outwards and Downwards,	External Rectus. Inferior Rectus. Superior Oblique.

The term *visual field* is given to the area intercepted by the extreme visual lines which pass through the centre of the pupil, the amount of dilatation of which determines its size. It follows the movements of the eye, and is displaced with it. Each point in the visual field has a corresponding point on the retina; but the portion, as already explained, which secures our attention, is that falling on the yellow spot.

7. BINOCULAR VISION.

When we look at an object with both eyes, its image falls upon the two yellow spots, and it is seen as one object. If, however, we displace one eyeball by pressing it with the finger, then the image in the displaced eye does not fall on the yellow spot, and we see *two* objects, one of them being less distinct than the other. It is not necessary, however, in order to see a single object with two eyes that the two images fall on the two yellow spots; an object is always single if its image fall on *corresponding points* in the two eyes. Thus, in the experiment above described, after having seen two images by displacing one eyeball, we may be able again to see only one image by pressing on the other eyeball. There are then corresponding points in the two retinæ, so that if they were superposed, the two yellow spots would coincide; the upper and lower parts of the left retina would touch the upper and lower parts of the right retina; the nasal side of the left retina would correspond to the temporal side of the right retina; and the reverse would also hold good. Thus, in Fig. 164, an object at a'' or at b'' or at c'' will be seen singly by the two eyes A and B, as the images fall on corresponding points in the retinæ, namely, $a\ a'$ $b\ b'$ and $c\ c'$. It will be observed that if the eye B were displaced, the images would not fall on corresponding points, and consequently two would be seen. The name *horopter* has been given to a line connecting those points in the visual field which form their image on corresponding points of the retina. The older physiologists first gave this name to "a straight line or plane passing through the point of convergence of the axes of the eyes, or the point to which the eyes are directed," but Vieth and Müller showed that it cannot be a straight line or plane, but must have a circular form. Thus if the points *a b c* in Fig. 164 correspond to the points $a' b' c'$, the angles 4 and 1 in the one eye must correspond to the angles 4 and 1 in the other. Then *a b* being equal to $a' b'$, the angle 1 in eye A equal to angle 1 in eye B, the angles $1'$ and $1'$ will be equal. Since the angles 2 and 2 are equal, the angles 3 and 3 must also be equal. In the same way, the angle 5 is equal to angle 3. For $b\ c = b'\ c'$, and angle 4 = angle 4. Thus the angles 3, 3, and 5 are equal, and $a''\ b''\ c''$ cannot lie in a straight line, for it is the property of a circle only that triangles erected on the same chord, and reaching the periphery, have at the periphery equal angles (Müller's Physiology, vol. ii., p. 1195). A line joining $a''\ b''\ c''$ is therefore the horopter, and its form is illustrated by Fig. 165. It is therefore a circle, of which the chord is formed by the distance between the points of decussation of the rays of light in the eye. Its size is determined by the position of the two eyes, and the point towards which their axes converge. Thus, if A in Fig. 164 were nearer the eyes, the horopter would be the chord of a smaller

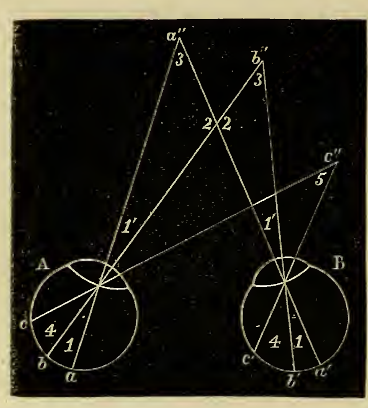


Fig. 164.—Diagram to illustrate theory of corresponding retinal points.

circle. The form of the horopter in the tertiary positions of the eyeball is extremely complicated.

All objects which are not found in the horopter, or, in other words, do not form an image on corresponding points of the retinæ, are seen double. When the eyeballs are so acted upon by their muscles as to secure images on non-corresponding points, and consequently double vision, the condition is termed *strabismus*, or squinting, of which there are several varieties, treated of in works on ophthalmic surgery.

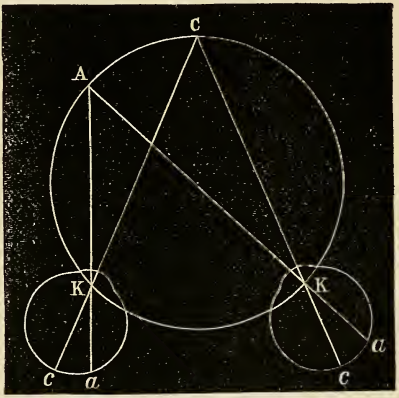


FIG. 165.—Diagram to illustrate the horopter.

It is important to observe that in the fusion of double images we must assume not only the correctness of the theory of corresponding points of the retina, but also that there are corresponding points in the brain, at the central ends of the optic fibres. Such fusion of images may occur without consciousness; at all events it is possible to imagine that the cerebral effect (except as regards consciousness) would be the same when a single object was placed before the two eyes, in the proper position, whether the individual were conscious or not. On the other hand, as we are habitually conscious of a single image, there is a psychical tendency to fuse double images when they are not too dissimilar.

Binocular vision may be illustrated by the following experiment: Take two No. 3 eye-pieces of a Hartnack's microscope, place one in front of each eye, direct them to a clear window, in daylight, and two luminous fields will be seen, one corresponding to each eye. Then converge the two eye-pieces until the two luminous circles cross, and the central part, like a bi-convex lens, will appear clear and bright, while the outer segments will be much less intense, and may appear even of a dim grey colour. Here, evidently, the sensation is due to a fusion of impressions in the brain. With a similar arrangement, blue light may be admitted by the one eye-piece and red by the other, and on the convergence of the two, a resultant colour, purple, will be observed. This may be termed the binocular vision of colours.

8. Psychical Relations of Vision.

Hitherto we have considered (1) the anatomical arrangements of the eye; (2) the nature of the stimulus acting on it; (3) the optical arrangements by which the stimulus is enabled to act directly on the retina; (4) the specific action of light on the retina; and (5) the mechanical arrangements by which single vision with two eyes is secured. The sense of vision, however, plays so important a part in our psychical states, and bears so evident a relation to all our movements, as to merit further attention.

a. *Characters of Visual Perceptions.*

All visual perceptions, if they last for a sufficient length of time, appear to be external to ourselves, erect, localized in a position in space, and more or less continuous.

1. *Visual Sensations are referred to the Exterior.*—This appears to be due, to a large extent, to habit. Those who have been born blind, on obtaining eyesight by an operation, have imagined objects to be in close proximity to the eye,

and they have not had the distinct sense of exteriority which most individuals possess. Slowly, and by a process of education, in which the sense of touch played an important part, they gained the knowledge of the external relations of objects. Again, phosgenes, when first produced, appear to be in the eye; but, when conscious of them, by an *imaginative* effort, we may transport them into space; yet they never appear very far off.

2. *Visual Sensations are referred to Erect Objects.*—Although the images of objects are *inverted* on the retina, we see them erect. The explanation of the effect is, that we are conscious not of the image on the retina, but of the luminous object from which the rays proceed, and we refer the sensation in the *direction* of these rays. Again, in running the eye over an object, say a tall pole, from base to apex, we are not conscious of the different images on the retina, but of the muscular movements necessary to bring the parts successively on the yellow spot.

3. *Visual Sensations are referred to a Position in Space.*—The localization of a luminous point in space can only be determined by observing its relations to other luminous points with a given position of the head and of the eye. For example, in a perfectly dark room, if we look at a single luminous point, we cannot fix its exact position in space, but we may get some information, of a vague character, by moving the head or the eye. If, however, a second luminous point appear in the darkness, we can tell whether it is nearer or farther distant, above or below, the first. So with regard to other luminous points: we observe their reciprocal relations, and thus we localize a number of visual impressions.

4. *Visual Sensations are Continuous.*—Suppose the image of a luminous line falls on the retina, it will appear as a line although it is placed on perhaps 200 cones or rods, each of

which may be separately excited, so as to cause a *distinct* sensation. Again, on the same principle, the impression of a superficial surface may be regarded as a kind of *mosaic*, made up of individual portions corresponding to the rods or cones on which the image of the surface falls. But in both cases the sensation is continuous, so that we see a line or a surface. The individual images are fused together.

b. *Notions derived from Visual Perceptions.*

When we look at any object, we judge of its size, the direction of its surfaces (unless it be a point), its distance from the eye, its apparent movement or fixedness, and its appearance of solidity.

1. *Apparent Size.*—This, so far as regards a comparatively small object, depends on the size of the retinal image, as determined by the visual angle. With a very large object, there is an appreciation of size from the muscular sensations derived from the movements of the eyeball, as we "range" the eye over it. It is difficult to appreciate the distance separating two points between which there are other points, as contrasted with an apparently similar distance without intermediate points. For example, the distance A to B appears to be greater than from B to C in Fig. 166, although the two distances are equal.

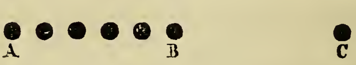


Fig. 166.—Illusions of size.

2. *Direction.*—As the retina is a curved surface, a long straight line, especially seen from a distance, appears curved. In Fig. 167 a curious illusion of direction, first shown by Zoellner, is depicted. If these lines be looked at somewhat obliquely, say from one corner, they will appear to converge or diverge, and the oblique lines, on each side of the vertical lines, will appear not to be exactly opposite each other. But the vertical lines are parallel, and the oblique lines are continuous across them. The effect is evidently due to an error of judgment, as it may be controlled by an intense effort, when the lines will be seen as they really are.

Fig. 167.—Zoellner's Figure, showing an illusion of direction.

3. *Apparent Distance.*—We judge of distance, as regards large objects at a great distance from the eye, (1) from their apparent size, which depends on the dimensions of the visual angle; and (2) from the interposition of other objects

between the eye and the distant object. Thus, at sea, we cannot form, without great experience, an accurate estimate of how many miles we are off the coast, and all know how difficult it is to estimate accurately the width of a river. But if objects be interposed between the eye and the distant object, say a few vessels, at different distances, at sea, or a boat in the river, then we have certain materials on which to form a judgment, the accuracy of which, however, even with these aids, will depend on experience. When we look at a near object, we judge of its distance chiefly by the sense of effort put forth in bringing the two lines of regard (see p. 597) to converge upon it.

4. *The Movement of a Body.*—If the eye be fixed, we judge of movement by successive portions of the retina being affected, and possibly also by a feeling of an *absence* of muscular contractions necessary to move the eyeballs. When the eye moves so as to "follow" the object, there is a sense of muscular effort, which is increased when, in addition, we require to move the head.

5. *The Apparent Solidity of an Object.*—If we look at an object, say a cube, first with the right eye and then with the left, it will be found that the two images of the object are somewhat different, as in Fig. 168.

FIG. 168.—Illustrating stereoscopic vision.

If, then, by means of a stereoscope, or by holding a card between the two eyes and causing a slight convergence of the eyes, the two images are brought upon corresponding points of the two retinæ, the image will be at once seen in relief.

Consult, regarding the eye, as the most important treatise, Optique Physiologique, by HELMHOLTZ, 1867; also MACKENZIE on the Eye and Vision, 1841. In the first-mentioned treatise, a full list is given at the end of each section of all the more important works of reference regarding the eye up to its date.

F.—SENSE OF HEARING.

1. Anatomical Conditions.

The ear consists of an apparatus specially fitted for the transmission of sonorous vibrations to the terminal apparatus of the auditory nerve. Its description is found in any anatomical work. From the physiological point of view, its various parts are shown in the following diagram (Fig. 169).

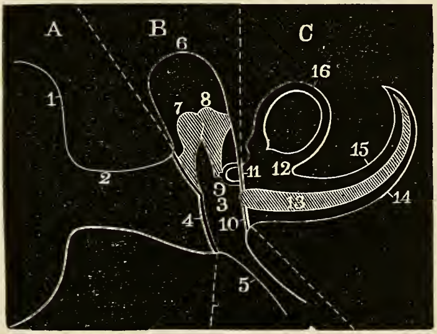


Fig. 169.—Diagrammatic view of the auditory apparatus (*Beaunis*). A, external ear; B, middle ear; C, internal ear. 1, concha; 2, external auditory passage; 3, tympanum; 4, membrana tympani; 5, Eustachian tube; 6, mastoid cells; 7, malleus; 8, incus; 9, stapes; 10, fenestra rotunda; 11, fenestra ovalis; 12, vestibule; 13, cochlea; 14, scala tympani; 15, scala vestibuli; 16, semicircular canal.

It consists of the following parts: (1) the external ear, formed of the *concha*, and *external auditory canal;* (2) the middle ear, a cavity filled with air, communicating with the back of the throat by the *Eustachian tube*, and separated from the external ear by the *membrana tympani*, the latter being connected with the *fenestra ovalis* by a chain of bones, namely, the *malleus*, *incus*, and *stapes;* and (3) the internal ear or labyrinth, a complicated structure filled with fluid, and consisting of the *vestibule*, *semicircular canals*, and the *cochlea*.

The essential part of the auditory apparatus is the internal ear, or *labyrinth*. This is divided into three parts, as represented in Fig. 170. These are, the three semicircular canals on the one side, the cochlea on the other, and the vestibule between the two. The wall of the latter is pierced by an opening, the *fenestra ovalis*, *d*, closed by a membrane, into which is inserted the base of the stapes. Seven openings communicate with the vestibule, viz., the fenestra ovalis, five orifices of the semicircular canals, and an aperture communicating with the scala vestibuli of the cochlea. The vestibule contains masses of crystals of calcareous matter called *otoliths*. From its walls, hair-like bodies project, which arise from cells connected with the extremities of the vestibular division of the auditory nerve.

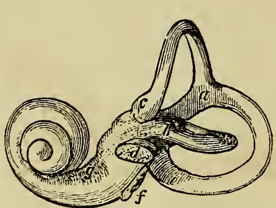


FIG. 170.—Diagrammatic view of the osseous labyrinth. See text.

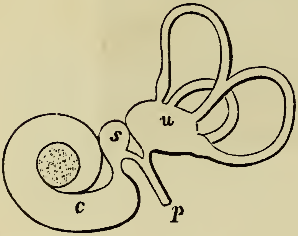


FIG. 171.—Membranous labyrinth. See text.

The osseous labyrinth contains a membranous structure, termed the membranous labyrinth, seen in Fig. 171. This consists of two sacs—the utricle, *u*, communicating with the semicircular canals, and the saccule, *s*, opening into *c*, the ductus cochlearis

It will be observed that *s* and *u* communicate by a forked canal which is said to be lodged in the aquæductus vestibuli of the temporal bone.

The semicircular canals have been termed the *anterior vertical,* a dilatation of which, termed the ampulla, is seen at *c;* the *posterior vertical, e;* and the *horizontal, b* (Fig. 170). It will be observed that the anterior and posterior vertical open into the vestibule by a common tube, *a.*

The cochlea may be regarded as a tube, tapering towards one extremity, twisted round a central axis or *columella.* This tube is divided into two cavities by a spiral partition formed of two parts, one osseous, next the columella, and the other membranous, which completes the division, as seen in Fig. 172, which represents a section of the osseous part of the cochlea. In this figure, *b* is the columella or axis, round which the spiral partition of bone, *a c,* is twisted. From the edge of the osseous partition (termed the *lamina spiralis*) two membranes pass obliquely, so as to cut off a triangular space, the *scala intermedia.* The position of this space, in which exists the most important part of the terminal apparatus of hearing, is indicated in the diagram, Fig. 173. From the free edge of the osseous lamina spiralis, Ls, a membrane, *b,* the *basilar membrane,* passes transversely across to a set of fibres, Lsp, sometimes called the ligament of the lamina spiralis, or *Bowman's muscle.* A second mem-

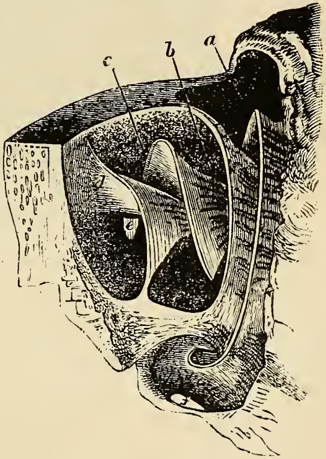


Fig. 172.—Section of the cochlea. See text.

brane, V, *Reissner's membrane,* passes from Ls to the osseous wall of the tube. The tube is thus divided into three parts, viz., *scala vestibuli,* Sv, communicating with the vestibule;

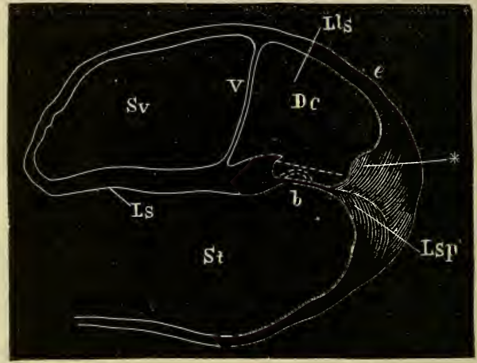


Fig. 173.—Diagram showing a section of the tube of the cochlea. See text.

scala tympani, St, communicating with the tympanum through the *fenestra rotunda* (see Fig. 169, 10); and between the two a third space, Dc. The space between *b* and V is frequently spoken of as the cochlear canal, and on *b*, the

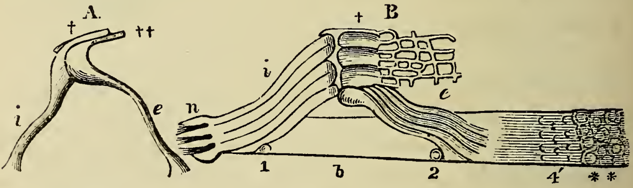


Fig. 174.—Corti's organ. A, profile view of two rods, *i* internal, *e* external. B represents in position five complete arches resting on the basilar membrane *b*. For further description see Quain's Anatomy, vol. II., p. 657.

basilar membrane, we find the *rods of Corti,* forming a series of arches for the support of certain cells having hair-like appendages, which latter are the true vibratory organs of hearing. The general arrangement of the rods is seen in Fig. 174. The rods support a number of modified epithelial cells, termed *hair cells*, because they bear minute hair-like structures. In man, there are five rows of such cells over the external and one over the internal rods. It is difficult to see these cells in the cochlea of mammals, but they may be observed with greater facility in birds, where they rest directly on the basilar membrane, no arches of Corti being present. In Fig. 175 hair-cells, *d*, are seen as found in the cochlea of a pigeon. It will be observed that they are connected by delicate filaments with nucleated cells, *b;* also with such a multipolar nerve-cell as *c;* and that they rest on a basilar membrane, *a*.

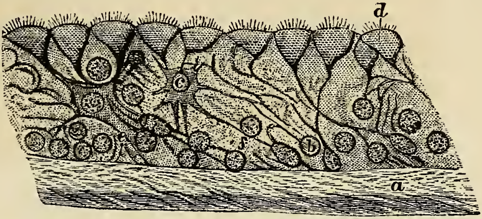


FIG. 175.—Portion of cochlea of pigeon, showing hair cells. See text. (*Paul Meyer.*)

2. Physical Causes of Sound.

Sonorous vibrations consist of the regular to-and-fro movements or oscillations of any elastic body. When such vibrations are communicated to the ear with sufficient rapidity and intensity, the result is an auditory sensation called a sound. Sound is usually conveyed to the ear by the air, but it may also be conveyed through solids and liquids. The movements of a sounding body, say a tuning-fork, may be shown graphically by recording them on a surface (Fig.

2, p. 88). The to-and-fro movements of the molecules of any elastic body constitute a vibration or oscillation. Different points of a medium traversed by a vibratory movement pass successively through the same phases, and in applying the term *wave*, it is important not to confound it with the vibrations of the individual molecules. The term "*wave-length*" is the distance which separates two points of a vibrating body, found at the same *instant* in the same phase. The wave-length is constant for a given number of vibrations in a second in the same medium, and it is proportional to the duration of the vibration, and in the inverse ratio to its rapidity.

Sounds may be classified into *noises* and *musical tones*. A noise is a sensation produced by non-periodic motions against the ear, or by a number of musical tones clashing together, so as to cause dissonance, as when we bring the palm of the hand down at random on the key-board of a piano.

A *tone* is produced by a periodic movement of the air or of the sounding body. Its production is well illustrated by the double syren of Helmholtz, shown in Fig. 176. It consists of two brass boxes, a_0 a_1, communicating with a powerful bellows by the tubes g_0 and g_1. The lids of these boxes are perforated by a number of holes. Adjusted to the lids, there are two perforated brass discs, moving on a common spindle, k. The holes in the lower disc are seen over the lower box in the figure, but not in the upper. These holes pass through the lid of the box and through the discs obliquely in opposite directions, so that when air is forced by the bellows out of the boxes, the discs are driven round. As the discs revolve, when the holes in the disc and in the lid of the box coincide, the air escapes; the disc is driven onwards, thus bringing its unperforated parts over the holes, so that the air cannot escape. "Hence the continuous stream of air from the bellows is converted into a series of discontinuous puffs, which, when they follow one

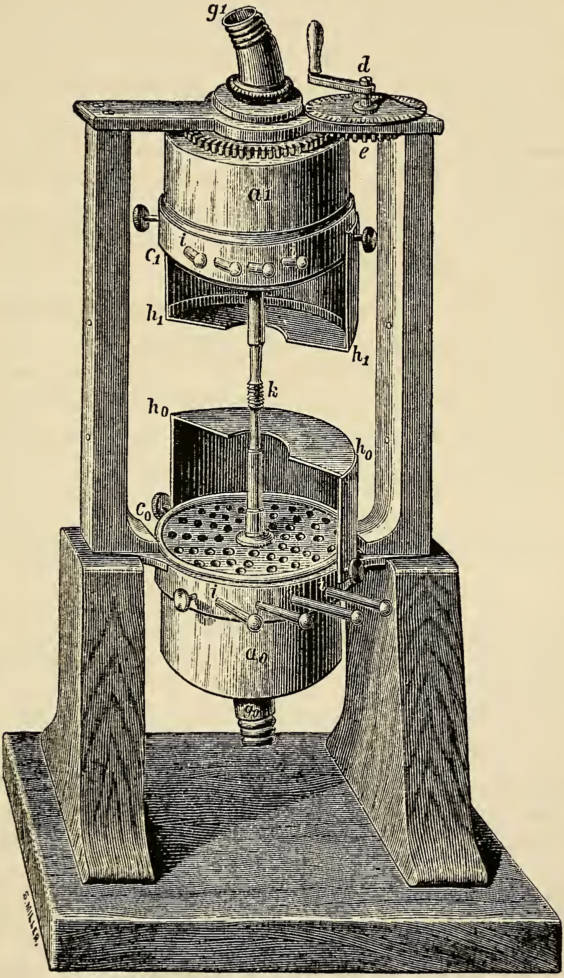


Fig. 176.—Double syren of Helmholtz. See text.

another with sufficient rapidity, gather themselves into a tone. Thus it can be shown that a *tone* depends on a regular series of equal impulses reaching the ear, or on a periodic movement of the air. By this instrument, also, the relations of sounds, as expressed by *intervals*, can also be shown. In each disc there are four concentric rows of holes, and by means of the stops marked *i* and *i*, any of these may be opened. In the lower box, the stops are marked 8, 10, 12, 18, and in the upper, 9, 12, 15, and 16, indicating the number of holes respectively. Suppose the row marked 16 is opened, at first a series of puffs are heard, but these soon fuse together in consciousness, so as to cause the sensation of a *pure tone.* When the puffs come at the rate of about thirty per second, a tone is heard. Again, we can use any one of the eight series of holes, or combine them as we wish. Suppose we open the row of holes marked 8 and the row marked 16, then we have two sounds produced in the relation of an octave.

3. Arrangements for Transmission of Vibrations to the Terminal Organ.[1]

Hearing is a special sensation, the cause of which is an excitation of the auditory nerves by the vibrations of sonorous bodies.

a. *Transmission in External Ear.*

The external ear consists of the *pinna* or auricle, and the *external auditory meatus* or canal, at the bottom of which we find the *membrana tympani* or drum head. In many

---

[1] The account of the physiology of hearing here given was written by the author for the Encyclopædia Britannica, 9th edition, article "Ear," and is here reproduced with few alterations by the kind consent of the publishers, Messrs. A. & C. Black.

animals the auricle is trumpet-shaped, and, being freely moveable by muscles, serves to collect sonorous waves coming from various directions. The auricle of the human ear presents many irregularities of surface. If these be abolished by filling them up with a soft material such as wax or oil, leaving the entrance to the canal free, experiment shows that the intensity of sounds is weakened, and that there is more difficulty in judging of their direction. When waves strike the auricle, they are partly reflected outwards, whilst the remainder, impinging at various angles, undergo a number of reflections, so as to be directed into the auditory canal. Vibrations are transmitted along the auditory canal, partly by the air it contains, and partly by its walls, to the membrana tympani. The absence of the auricle, as the result of accident or intentional injury, has not caused diminution of hearing. In the auditory canal, waves of sound are reflected from side to side, until they reach the membrana tympani. From the obliquity in position and peculiar curvature of this membrane, most of the waves must strike it nearly perpendicularly, that is, in the most advantageous direction.

b. *Transmission in Middle Ear.*

The middle ear is a small cavity, the walls of which are rigid, with the exception of the portions consisting of the membrana tympani and the membrane of the round window (*fenestra rotunda*), and of the apparatus filling the oval window (*fenestra ovalis*). This cavity communicates with the pharynx by the Eustachian tube, which forms a kind of air-tube between the pharynx and the tympanum, for the purpose of regulating pressure on the membrana tympani. It is generally supposed that during rest the tube is open, and that it is closed during the act of deglutition. As this action is frequently taking place, not only when food or drink is introduced, but when saliva is swallowed, it is evident that the pressure of the air in the tympanum will be kept in a state of equilibrium with that of the external air, exerted on the outer surface of the membrana tympani, and that thus the latter will be rendered independent of variations of atmospheric pressure, such as may occur within certain limits, as when we descend the shaft of a mine or ascend a high mountain. By a forcible expiration, the oral and nasal cavities being closed, air may be driven into the tympanum, while a forcible inspiration (*Valsalva's experiment*) will draw air from that cavity. In the first case, the membrana tympani will bulge outwards; in the second case, inwards; and in both, from excessive stretching of the membrane, there will be partial deafness, especially for sounds of high pitch. Permanent occlusion of the tube is one of the most common causes of deafness.

The membrana tympani is capable of being set into vibration by a sound of any pitch included in the range of perceptible sounds. It responds exactly, as to number of vibrations (pitch), intensity of vibrations (loudness), and complexity of vibration (quality or timbre). Consequently we can hear a sound of any given pitch, of a certain intensity, and in its own specific timbre or quality. Generally speaking, very high tones are heard more easily than low tones of the same intensity. As the membrana tympani is not only fixed by its margin to a ring or tube of bone, but is also adherent to the handle of the malleus, which follows its movements, its vibrations meet with considerable resistance. This diminishes the intensity of its vibrations, and prevents also the continued vibration of the membrana after an external vibration has ceased, so that a sound is not heard much longer than the moment when the exciting cause ceases. The tension of the membrane may be affected (1) by differences of pressure on the two surfaces of the membrana tympani, as may occur during forcible expiration, or inspiration, or in a pathological condition; and (2) by muscular action due to contraction of the *tensor tympani* muscle. This small muscle arises from the apex of the petrous temporal and the cartilage of the Eustachian tube, enters the tympanum at its anterior wall, and is inserted into the malleus near its root. The handle of the malleus is inserted between the layers of the membrana tympani, and as the malleus and incus move round an axis, as seen in Fig. 177, passing through the neck of the malleus, from before backwards, the action of the muscle is to pull the membrana tympani inwards towards the tympanic cavity, in the form of a cone, the meridians of which, according to Helmholtz, are not straight but curved, with convexity outwards. When the muscle contracts, the handle of the malleus is drawn still farther inwards, and thus a greater tension of the tympanic membrane is produced. On relaxation of the muscle, the membrane returns to its position of equilibrium, by its own elasticity, and by the elasticity of the chain of bones. This power of varying the tension of the membrane is a kind of accommodating mechanism for receiving and transmitting sounds of different pitch. With different degrees of tension, it will respond more readily to

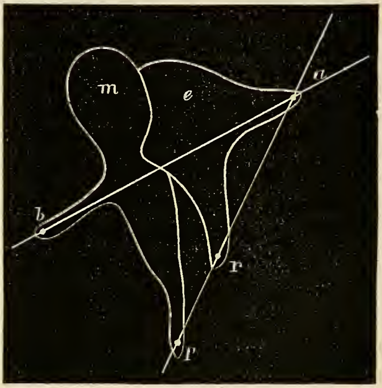


FIG. 177.—Diagram showing the axis of rotation of the bones of the ear. *m*, malleus; *e*, incus; *a*, short process of incus, abutting against tympanic wall; *r*, long process of incus, bearing the stapes; *p*, handle of the malleus; *a b*, axis of movement.

sounds of one pitch than to sounds of another. Thus, when the membrane is tense, it will readily respond to high sounds, while relaxation will be the condition most adapted for low sounds. In addition, increased tension of the membrane, by increasing the resistance, will diminish the intensity of vibrations. This is especially the case for sounds of low pitch. Helmholtz has also pointed out that the peculiar form of the membrana tympani in man has the effect of increasing the force of its vibrations at the expense of their amplitude.

The vibrations of the membrana tympani are transmitted to the internal ear partly by the air which the middle ear, or tympanum, contains, and partly by the chain of bones consisting of the malleus, incus, and stapes. Of these, transmission by the chain of bones is by far the most important. In birds and in the scaly amphibia, this chain is represented by a single rod-like ossicle, the *columella;* but in man the two membranes, membrana tympani and the membrane of the fenestra ovalis, are connected by a compound lever, consisting of three bones, namely, the *malleus* or hammer, inserted into the membrana tympani; the *incus* or anvil; and the *stapes* or stirrup, the base of which fits into the oval window. The lever thus formed has its fulcrum at the short process of the incus, which abuts against the tympanic wall; the power is applied to the handle of the malleus, and the resistance is at the base of the stirrup. Both by direct experimental observation, and by calculation from data supplied by measurement of the lengths of the arms of the lever, Helmholtz has shown that, by this arrangement, vibrations are diminished in extent in the ratio of 3 to 2, but are inversely increased in force. Considering the great resistance offered to excursions of the stapes, and the small dimensions of the internal ear, such an arrangement must be advantageous. It must also be noted that in the transmission of vibrations of the membrana tympani to the fluid in the labyrinth or internal ear through the oval window, the chain of ossicles vibrates as a whole and acts efficiently, although its length is only a small fraction of the wavelength of the sound transmitted. The mechanical arrangements of the ossicles may be readily studied with the aid of the model devised by Helmholtz, shown in Fig. 178.

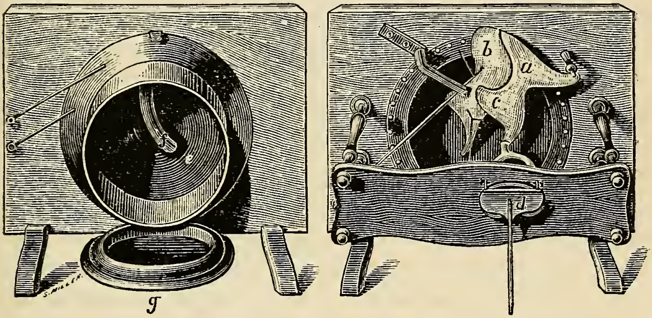


Fig. 178.—Model of the mechanical arrangements of the bones of the ear. External view to the left, internal to the right. *e*, in left-hand figure, outer surface of drum head, made of leather; *g*, cap, having india-rubber edge fitting over *e*, so that by compression, *e* may be caused to move. *a*, in right-hand figure, incus, showing its short process attached to tympanic wall, and its longer process, bearing the stapes; *b*, malleus; *d*, piece of wood bearing a wire, attached to oval window.

c. *Transmission in the Internal Ear.*

The internal ear is composed of the labyrinth formed of the *vestibule* or central part, the *semicircular canals*, and the *cochlea*, each of which consists of an osseous and of a membranous portion. The *osseous* labyrinth may be regarded as an osseous mould in the petrous portion of the temporal bone, lined by tesselated endothelium, and containing a small quantity of fluid called the *perilymph*. In the mould, partially surrounded by, and to some extent floating in, this fluid, there is the *membranous* labyrinth, in certain parts of which we find the terminal apparatus in connection with the auditory nerve, immersed in another fluid, called the *endolymph.* The membranous labyrinth consists of a vestibular portion, formed by two small sac-like dilations (see Fig. 171), called the *saccule* and the *utricle,* the latter of which communicates with the semicircular canals by five openings. Each canal consists of a tube, bulging out at each extremity, so as to form the so-called *ampulla,* in which, on a projecting ridge, called the *crista acoustica,* there are cells bearing, or developed into, long auditory hairs, which are to be regarded as the peripheral end-organs of the vestibular branches of the auditory nerve. The cochlear division of the membranous labyrinth consists of the *ductus cochlearis,* a tube of triangular form, fitting in between the two cavities in the cochlea, the one called *scala vestibuli,* because it commences in the vestibule; and the other, *scala tympani,* as it ends in the tympanum at the round window. These two scalæ communicate at the apex of the cochlea. The roof of the ductus cochlearis is formed by a thin membrane, called the *membrane of Reissner,* while its floor consists of the *basilar membrane,* on which we find the *organ of Corti* (see Figs. 169 and 173), which constitutes the terminal organ of the cochlear division of the auditory nerve.

Sonorous vibrations may reach the fluid in the labyrinth by three different ways: (1) by the osseous walls of the labyrinth; (2) by the air in the tympanum acting on the round window; and (3) by the base of the stapes inserted into the oval window.

When the head is plunged into water, or brought into direct contact with any vibrating body, vibrations are transmitted *directly.* Vibrations of the air in the mouth and in the nasal passages are also directly communicated to the walls of the cranium, and thus pass to the labyrinth. In like manner, we may experience peculiar auditive sensations, such as blowing, rubbing, and hissing sounds, due to muscular contraction or to the passage of blood in vessels close to the auditory organ. It has not been satisfactorily made out to what extent, if any, vibrations may be communicated to the fluid in the labyrinth by the round window. There can be no doubt, however, that in ordinary hearing vibrations are communicated chiefly by the chain of bones. When the base of the stirrup is pushed into the oval window, the pressure in the labyrinth increases, the impulse passes along the scala vestibuli to the scala tympani, and as the only mobile part of the wall of the labyrinth is the membrane covering the round window, this membrane is forced outwards; when the base of the stirrup passes outwards, a reverse action takes place. Thus the fluid of the labyrinth may receive a series of pulses or vibrations isochronous with the movements of the base of the stirrup, and these pulses affect the terminal apparatus in connection with the auditory nerve.

Since the size of the membranous labyrinth is small, measuring in man not more than $\frac{1}{10}$th of an inch in diameter at its widest part, and since it is a chamber consisting partly of conduits of irregular form, it is impossible at present to state precisely the course of vibrations transmitted to it by impulses communicated from the base of the stirrup. In the cochlea, vibrations must pass from the saccule along the scala vestibuli to the apex, thus affecting the membrane of Reissner, which forms its roof; then, passing through the opening at the apex (the *helicotrema*), they must descend by the scala tympani to the round window, and affect in their passage the membrana basilaris, on which, as already stated, the organ of Corti is situated. From the round window, impulses may be reflected backwards, but how they affect the advancing impulses is not known. The problem is even more complex when we take into account the fact that impulses are transmitted simultaneously to the utricle and to the semicircular canals. The mode of action of these impulses upon the nervous terminations is unknown; but to appreciate critically the hypothesis which has been advanced to explain it, it is necessary, in the first place, to refer to some of the general characters of auditory sensation.

4. Physiological Characters of Auditory Sensations.

Certain conditions are necessary for excitation of the auditory nerve sufficient to produce a sensation. In the first place, the vibrations must have a certain *amplitude:* if too feeble, no impression will be produced. The minimum limit has been stated to be the sensation caused by the falling of a ball of pith, 1 milligramme in weight, upon a smooth surface, such as glass, from a height of 1 millimetre at a distance of 91 millimetres from the ear.

In the next place, an impulse must have a certain *duration.*

Lastly, as already stated, a certain *number* of impulses must be made in a given interval of time to excite a sensation of a musical tone. By the syren, it may be shown that the lower limit is marked by about 30 vibrations per second. It has been ascertained by various methods that the upper limit is somewhere about 30,000 vibrations per second. Beyond this limit, few ears can detect any sound, and none range beyond 35,000 per second.[1]

Thus, a sound may or may not be loud, or it may appear to be higher or lower as regards pitch; but, in addition, it

---

[1] König has constructed a series of steel cylinders slung on a wooden framework, by which, when they are struck so as to elicit sound, the upper limits of sensibility to pitch may be tested.

may have a certain quality, timbre, or klang, or the peculiar characteristic of a musical sound by which we identify it as proceeding from a particular instrument or from a particular human voice. *Intensity*, as may be proved optically, depends upon a greater or lesser amplitude of the vibration. Consequently there will be a corresponding amount of excitation of the terminal apparatus. Thus, a feeble sound will cause a smaller excursion of vibratory hairs than a loud sound. *Pitch*, as a sensation, depends on the number of vibrations in a given interval of time, or, in other words, on the length of time occupied by a single vibration. It may be absolute or relative. Most individuals can determine the relative pitch of a sound by referring it to the pitch of another sound which they have just heard. By the few who are distinguished in the possession of what may be termed the memory of sounds, a correct estimation of pitch may be given; but no experiments prove that any individual can at once detect absolute pitch. An experiment with the syren shows that variations in pitch glide into each other by insensible gradations; but it is not easy to state the capabilities of the human mind as regards small differences of pitch. It has been stated that practised musicians may detect the $\frac{1}{64}$ of a semitone, but this is far beyond average attainment. In musical composition, the sounds range from about 40 to 4000 vibrations per second, that is, a range of about six octaves.

The third peculiarity of musical tone is *quality*, *timbre*, or "*klang*," by which we identify it as proceeding from a particular instrument or from a particular human voice. This appears to depend physically on what is called the *form* of the wave. Many waves of sound that reach the ear are compound waves, built up of constituent waves, so that the wave has a special form. This may be illustrated by Fig. 179, which shows by the continuous line the form of the wave resulting from the combination of the two waves represented by dotted lines. The same fact is still further

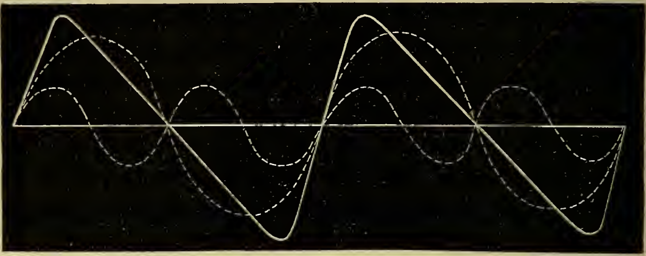


Fig. 179.—Form of wave produced by combining two simple waves.

illustrated by the following diagrams given by Helmholtz, Fig. 180.

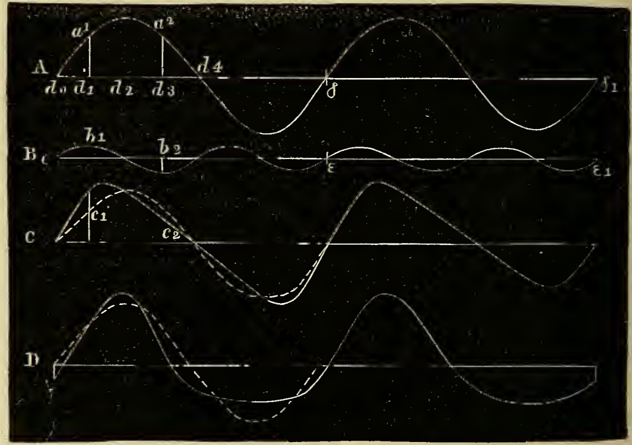


Fig. 180.—Various forms of wave curves. See text.

A and B represent waves of simple tones, B having twice the number of vibrations of A, or, in other words, an octave higher in pitch. By superimposing B on A, the curves C and D are produced. The dotted curves in C and D are representations of A. In C, the point e in B coincides with *do* in A; but in D, the deepest point, b_2 in B, is placed under the commencement of A. Thus, by starting B at different points, with reference to A, different wave-forms are produced.

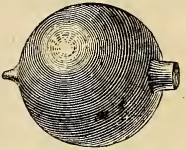


FIG. 181.—Resonator of Helmholtz.

Each of these constituent waves, however, may so affect the organ of hearing as to be perceived as individual sounds, more especially with the aid of an instrument called a *resonator*, shown in Fig. 181.

This consists essentially of a brass globe, having two openings, the narrower of which is placed in the external ear. Each resonator contains a mass of air which responds sympathetically to a particular tone. By using a number of such resonators, a compound tone may be analysed into its constituents, the action of an individual resonator being to strengthen the intensity of the tone to which it corresponds. Even without the aid of resonators, a sensitive ear may detect in the tone of a piano or harmonium some of its constituent tones. Thus it appears that the ear must have some arrangement by which it resolves any wave-system, however complex, into simple pendular vibrations. When we listen to a sound of any quality, we recognize that it is of a certain pitch. This depends on the number of vibrations of one tone, predominant in intensity over the others, called the *fundamental*, or first partial tone. Quality depends on the number and intensity of other tones, called partials, or *harmonics*, added to it. The relation of these to the first tone is very simple, their vibrational numbers being multiples of that of the fundamental tone, thus :—

	Fundamental Tone.	Upper Partials or Harmonics.								
Notes, . .	do^{1}	do^{2}	sol^{2}	do^{3}	mi^{3}	sol^{3}	si♭^{3}	do^{4}	re^{4}	mi^{4}
Partial tones,	1	2	3	4	5	6	7	8	9	10
Number of vibrations.	33	66	99	132	165	198	231	264	297	330

The relations of these tones, physically and physiologically, may be conveniently studied with the aid of tuning forks, such as is shown in Fig. 182. By combining the sounds of a series of such forks, the vibrational numbers of which are multiples of the first, various qualities of tone may be produced, and the effect of increased intensity of one tone over the others may also be illustrated. Thus, quality of tone may be studied *synthetically*. As already stated, compound tones may be analysed by means of resonators applied to the ear; but the same may be done optically with the aid of apparatus devised by Dr. König of Paris. The principle of his method will be readily understood with the aid of Fig. 183.

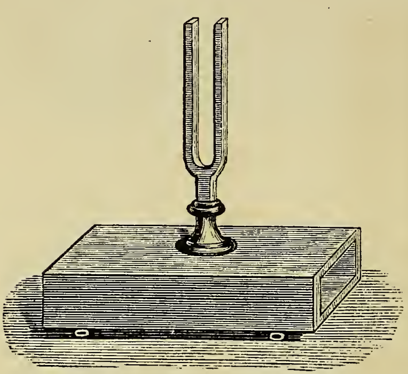


Fig. 182.—Tuning-fork mounted on resonance box, for increasing intensity of tone. The best tuning forks for the purpose are made by König.

A small wooden capsule, the base of which is formed of thin india-rubber membrane, is screwed over a circular hole in the side of an organ pipe. By means of tubes, ordinary gas is led into and from the capsule, and the tube leading from it is connected with a small gas burner. Thus the air in the organ pipe is separated from the gas by the thin membrane, so that the latter responds to every movement of the air, and consequently affects the pressure of the gas in the capsule. When such a pipe is sounded, the flame appears unsteady and of a pale blue colour, and if we then rotate a rectangular mirror, as suggested by Wheatstone, in front of the flame, a picture of the movements of the air in the pipes is seen on the mirror, such as is represented in Figs. 184 and 185.

If two organ pipes of the same pitch are employed, the teeth of the flame picture will be equal in number; but by using pipes giving the various intervals of the scale, the relations of these intervals may be shown optically. Thus, by combining a tone with its octave, the flame-picture shown in Fig. 185 will be produced.

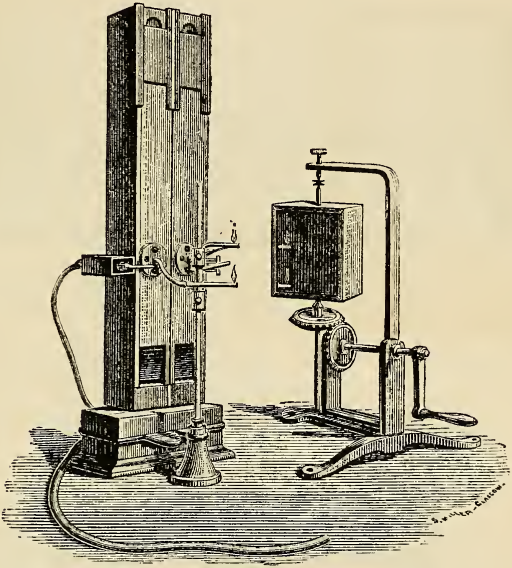


FIG. 183.—König's apparatus for studying optically the vibrations of the air in organ pipes. See text.

Taking advantage of this method of what he terms *manometric flames*, König has devised an ingenious apparatus, shown in Fig. 186, by which any compound tone, whose fundamental tone is $\text{UT}_2 = 256$ vibrations per second, may be analysed. No apparatus with which the author is acquainted shows to the student more clearly the physical conditions upon which quality depends. It consists of a series of resonators, each connected with its special flame, mounted on a cast-iron framework, the flames being reflected by an elongated rectangular mirror.

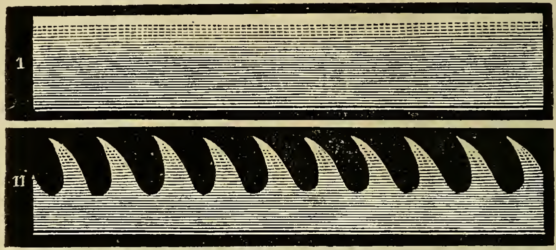


FIG. 184.—Appearance of the flame in the mirror of König's apparatus. 1, organ pipe not sounding; 2, organ pipe sounding,—the teeth representing individual vibrations of the air in the pipe.

On sounding any of the tuning forks in the harmonic series of UT$_2$ in front of this instrument, at the same time rotating the mirror, a special flame is affected, and appears segmented as represented in Fig. 185; and on producing any compound tone, the fundamental of which is UT$_2$, or which contains any harmonics of this series, it is at once analysed optically by the segmentation of the individual flames; also, on singing loudly

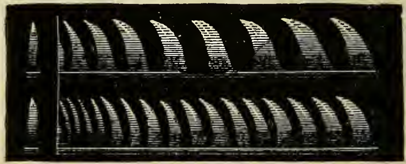


FIG. 185.—Flame-picture of two organ pipes sounding an octave. It will be observed that the teeth are in the ratio of 2:1. The erect figures to the left are reflections from a small stationary mirror, for purposes of comparison.

in front of the instrument, the tones of the human voice may be analysed.

When a simple tone, or one free from partials, is heard, it gives rise to a soft, somewhat insipid, sensation as may be

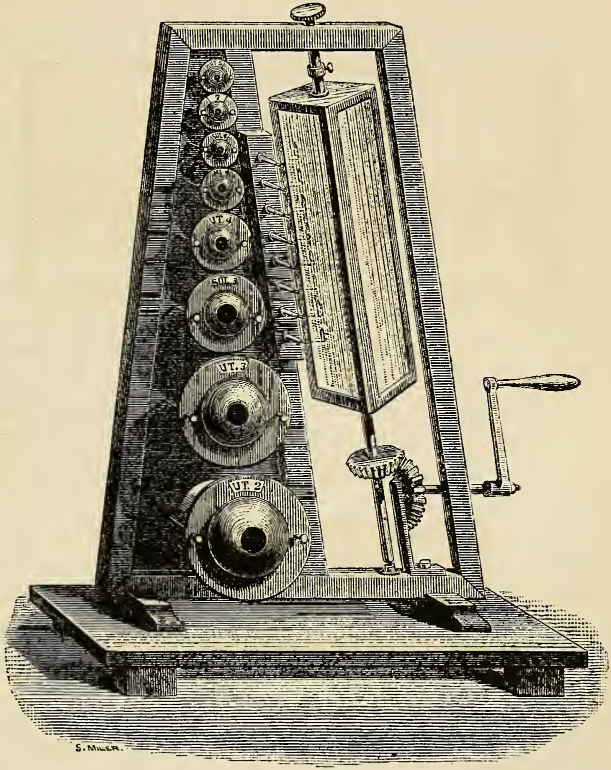


FIG. 186.—König's apparatus for the analysis of a compound tone, the fundamental of which is UT 2.

obtained by blowing across the mouth of an open bottle, or by a tuning fork. The lower partials added to the fundamental tone give softness combined with richness; while the higher, especially if they be very high, produce a brilliant and thrilling effect, as is caused by the brass instruments of an orchestra. Such being the facts, how may they be explained physiologically?

5. PHYSIOLOGICAL ARRANGEMENTS FOR THE APPRECIATION OF QUALITY OF TONE.

Little is known regarding the mode of action of the vibrations of the fluid in the labyrinth upon the terminal apparatus connected with the auditory nerve. There can be no doubt that it is a mechanical action, a true communication of impulses to delicate hair-like processes, by the movements of which the nervous filaments are irritated. In the human ear it has been estimated that there are about 3,000 small arches formed by the *Rods of Corti.* Each arch rests on the basilar membrane (see Fig. 174), and supports rows of cells, having minute hair-like processes, somewhat resembling cilia. It would appear also that the filaments of the auditory nerve terminate in the basilar membrane, and possibly they may be connected with the hair cells. At one time it was supposed by Helmholtz that these fibres of Corti were elastic, and that they were tuned for particular tones, so as to form a regular series corresponding to all the tones audible to the human ear. Thus, 2,800 fibres distributed over the tones of seven octaves, would give 400 fibres for each octave, or nearly 33 for a semitone. Helmholtz has put forward the ingenious hypothesis that when a pendular vibration reaches the ear, it excites by sympathetic vibration the fibre of Corti, which is tuned for its proper number of vibrations. If, then, different fibres are tuned to tones of different pitch, it is evident that we have here a mechanism which, by exciting different nerve fibres, will give rise to sensations of pitch. When the vibration is not simple but compound, in consequence of the blending of vibrations, corresponding to various harmonics or partial tones, the ear has the power of resolving this compound vibration into its elements. It can only do so by different fibres responding to the different vibrations of the sound, one for the fundamental tone being stronger, and giving the sensation of a particular pitch or height to the sound; and the others, corresponding to the upper partial tones, being weaker and causing special though undefined sensations, which are so blended together in consciousness as to terminate in a complex sensation, or a tone of a certain quality or timbre. It would appear at first sight that 33 fibres of Corti for a semitone are not sufficient to enable us to detect all the gradations of pitch in that interval; since, as has been stated above, trained musicians may distinguish a difference of $\frac{1}{64}$ of a semitone. To meet this difficulty, Helmholtz states that if a sound be produced, the pitch of which may be supposed to come between two adjacent fibres of Corti, both of these will be set into sympathetic vibration, but the one which comes nearest to the pitch of the sound will vibrate with greater intensity than the other, and that consequently the pitch of that sound would be thus appreciated. These theoretical views of Helmholtz have derived much support from remarkable experiments by Hensen, who observed that minute hairs on the antennæ of *Mysis*, a Crustacean, when observed with a low microscopic power, vibrated with certain tones produced by a keyed horn. It was seen that certain tones of the horn set some hairs into strong vibration and other tones other hairs. Each hair responded also to several tones of the horn. Thus one hair answered strongly to *d*♯ and *d′*♯, more weakly to *g* and very weakly to G. It was probably tuned to some pitch between *d″* and d″♯.

Recent histological researches have led to a modification of this hypothesis. It has been found that the rods or arches of Corti are stiff structures, not adapted for vibrating, but apparently forming a kind of support for the hair cells. It is also shown that there are no rods of Corti in the cochlea of birds, which apparently are capable nevertheless of appreciating pitch. Hensen and Helmholtz have now suggested the view that not only may the segments of the membrana basilaris be stretched more in the radial than in the longitudinal direction, but different segments may be stretched radially with different degrees of tension, so as to resemble a series of tense strings of gradually increasing length. Each string would then respond to a vibration of a particular pitch communicated to it by the hair cells. The exact mechanism of the hair cells and of the *membrana reticularis*, which suggests the idea of a damping apparatus, is unknown.

6. Psychical Characters of Auditory Sensations.

Under ordinary circumstances, auditory sensations are referred to the outer world. When we hear a sound, we associate it with some external cause, and it appears to originate in a particular place, or to come in a particular direction. This feeling of *exteriority* of sound seems to require transmission through the membrana tympani. Sounds which are sent through the walls of the cranium, as when the head is immersed in, and the external auditory canals are filled with, water, appear to originate in the body itself. It is probable, however, that the external character of ordinary auditory sensations may be more the result of habit than due to any anatomical peculiarity of the ear itself.

An auditory sensation lasts a short time after the cessation of the exciting cause, so that a number of separate vibrations, each capable of exciting a distinct sensation if heard alone, may succeed each other so rapidly that they are fused into a single sensation. If we listen to the puffs of a syren, or to vibrating tongues of low pitch, the single sensation is usually produced by about 30 or 35 vibrations per second; but there can be no doubt, as was first pointed out by Helmholtz, that when we listen to *beats* of considerable intensity, produced by two adjacent tones of sufficiently high pitch, the ear may follow as many as 132 intermissions per second.

The sensibility of the ear for sounds of different pitch is not the same. It is more sensitive for acute than for grave sounds, and it is probable that the maximum degree of acuteness is for sounds produced by about 3,000 vibrations per second, that is near fa^5♯. Sensibility as to pitch varies much with the individual and with the training to which he has subjected himself. The power of appreciating differences of pitch is termed a correct or just ear, and there can be no doubt of its improvement by cultivation.

7. Binaural Audition.

Hearing with two ears does not appear materially to influence auditive sensation, but probably the two organs are fitted for aiding us in determining the locality from whence a sound originates. It is asserted by Fechner that one ear perceives the same tone at a slightly higher pitch than the other, but this may probably be due to a pathological condition. If two tones, excited by two tuning forks of equal pitch, are produced one near each ear, there is a uniform single sensation; if one of the tuning forks be then made to revolve round its axis in such a way that its tone increases and diminishes in intensity, neither fork is heard continuously, but both sound alternately, the fixed one being audible only when the revolving one is not. It is difficult to decide whether excitations of corresponding elements in the two ears can be distinguished from each other. It is probable that the sensations may be distinguished, if one of the generating tones differ from the other in intensity or quality, although it may be the same in pitch. As has been shown by Silvanus P. Thompson, beats, due to interference, may be produced in the head by acting on the two ears *directly* by two tones of nearly the same pitch.

8. Musical Sensations.

Hitherto we have considered only the action of a single sound, but it is possible also to have simultaneous sensations, as in musical harmony and composition. It is impossible to ascertain what is the limit beyond which distinct auditory sensations may be perceived. When we listen to an orchestra, there is a multiplicity of sensations, and a total effect, but at the same time, we can single out and attentively notice the tones of one or two special instruments. Thus, the pleasure of music may arise partly from listening to simultaneous, and partly from the effect of contrast or suggestion in passing through successive, auditory sensations.

The principles of harmony belong to the department of music, but it is necessary to refer briefly to a few of these, from the physiological point of view. If two musical tones reach the ear at the same moment, an agreeable or disagreeable sensation is experienced, which may be termed a concord or a discord. It may be shown by the syren (in Fig. 176) that consonance and dissonance depend upon the ratio of the vibrational numbers of the two tones. The octave (1 : 2) the twelfth (1 : 3), and double octave (1 : 4), are absolutely consonant sounds; the fifth (2 : 3), is said to be perfectly consonant; then follow in the direction of dissonance, the fourth (3 : 4), major sixth (3 : 5), major third (4 : 5), minor sixth (5 : 8), and minor third (5 : 6). Helmholtz has attempted to account for this effect, more especially as regards compound tones, by the influence of *beats*.

Beats are observed when two tones of nearly the same pitch are produced together, and the number of beats per second is equal to the difference of the vibrational numbers of the two tones. They give rise to a peculiarly disagreeable intermittent sensation, comparable to what is experienced on watching a flickering light, an effect probably due to intermittent stimulation of the auditory nerve. Beats may be so rapid as not to be distinguished individually, but their existence gives a certain roughness to the tone. According to Helmholtz, the maximum roughness is attained by 33 beats per second. Above 132 per second, they are inaudible. When two notes are sounded, say on a piano, not only may the first, fundamental, or prime tones beat, but partial tones of each primary may beat also. Thus there may be a certain roughness of tone. If the partial tones of the prime tones coincide, there will be no beats; but if they do not coincide, the beats produced will give a peculiar character to the sensational effect of the interval. Thus in the octave and twelfth, all the partial tones of the acute sound coincide with the partial tones of the grave sound; in the fourth, major sixth, and major third, only two pairs of partial tones coincide; while in the minor sixth, minor third, and minor seventh, only one pair coincide.

Consult regarding the anatomy of the organ of hearing, QUAIN, vol. II., p. 626; STRICKER's Histology, vol. III., p. 1-200; PAUL MEYER, Études Histologiques sur le Labyrinthe Membraneux, Paris, 1876; regarding sound, TYNDALL, on Sound, 1867; SEDLEY TAYLOR, on Sound and Music, 1873; BLASERNA, The Theory of Sound in its Relation to Music, 1876; GAVARRET, Acoustique Biologique, Phenomènes Physiques de la Phonation et de l'Audition, 1877. For the fullest details regarding physiological acoustics, the student is referred to HELMHOLTZ's great work, Sensations of Tone, translated by ALEX. ELLIS, 1876.

G.—THE MUSCULAR SENSE.

By the muscular sense is understood the sensation produced by movements of muscles. This sensation may be either the perception of a voluntary effort being put forth to perform a certain movement, or it may be a feeling referred to various groups of muscles which are at the time in a state of movement. By means of it, we may gain information regarding the following points: (1) the *energy* of contraction; (2) the *extent* of contraction, by which we judge of precision of movement; (3) the *rapidity* of contraction; (4) the *duration* of contraction; and (5) the *position* of the members and of the body. The sense of *direction* of movement is complex, being made up of notions furnished by tactile, visual, and muscular sensations. By the muscular sense, also, we have a feeling of stability or equilibrium, a sensation which plays an important part in all movements. A feeling of muscular resistance aids us in the movements of locomotion, and in those adjustments of muscular effort which have to be made in delicate manipulations. We are aided by what may be termed a "guiding sensation." This may be derived from visual impressions or from muscular sensations, or from both combined. When the muscular sense is paralysed, as in *locomotor ataxia*, the patient guides his movements by looking at his feet, and when his attention is diverted, by causing him to look at something else, his gait becomes unsteady, or he may totter and fall.

It has not been decided whether or not there are special sensory nerves distributed to muscles. To account for the phenomena of the muscular sense, three theories have been advanced: (1) That we judge of the state of the muscles by the amount of effort necessary to cause a certain amount of contraction, that is, we perceive the intention or volition and not the phenomena following these; (2) That what we term *muscular sensations* are due to the excitation of nerves in the skin or membranes, serous or mucous, covering the muscles; and (3) That there are special sensory nerves distributed to the muscles which convey impressions directly to the nerve centres. The latter view is the one most generally adopted.

SLEEP, DREAMS, SOMNAMBULISM, ETC.

Like other organs, the brain manifests periodicity of function, so that we have the two states of wakefulness and sleep. The desire for sleep comes on at more or less regular intervals, and is accompanied by many sensations which scarcely even require enumeration: the heaviness of the eyes—in other words, the muscular sensations referable to the *levator palpebræ superioris;* the sensations referred to the muscles of the throat which precede a yawn; the heaviness of the head and of the limbs; and the apparently enfeebled effect of sensory impressions. Then ensues a more or less unconscious state, which affects to a certain degree all the other functions. Thus the pulse is slower, the respiratory movements fewer in number and more profound, the amount of carbonic acid eliminated is diminished, and digestion goes on more slowly. This state continues for several hours, or perhaps only for a few minutes; but whether of long or short duration, the period of its access and the period of its disappearance have the same psychological characters, namely, lessened acuteness to sensory perception, a confusion of ideas, and a loss of mental control.

The physiological cause of sleep cannot at present be stated. So far as one can judge from observations made during sleep on the surface of the brain and on the retinal expansion, there appears to be a state of cerebral anæmia, that is, less blood is found in the vessels. No hypothesis at present advanced explains all the phenomena of sleep.

Dreams are indications of partial cerebral activity. During profound sleep there are no dreams; they occur when slumber is light, and consequently they are more apt to happen during the time when the person passes from profound sleep to wakefulness. In dreaming, the ideas are under no control; old sensations crowd upon the mind in confusion and unconnected; notions of time and space are vague or entirely absent; in our supposed actions, we are guided by transient impulses, without definite moral notions, so that when we awake there is a feeling of relief that it was all a dream. If we watch a dreamer, he may be seen to move his lips or even to utter sounds, or to toss his arms to and fro—actions indicating the influence of his partially-active cerebral centres. Here is the transitional step from dreaming to *somnambulism*. In some persons, the ideas of the dream become so intense and definite as to result in movements of locomotion. The walking dreamer then may perform very definite movements: he may be regarded as acting his dream. In such circumstances, he may be influenced by suggestions from without. By a word whispered into his ear in the tones of a well-known voice, if the suggestion coincide with the train of ideas in the dream, the dreamer may be led to another line of conduct.

During sleep which is not profound, the current of the dream may be affected by many kinds of bodily states. Those coming from the digestive organs may give rise to a feeling of intense oppression, referred to the chest, and usually associated with dreaming of a horrible character—a state known as *nightmare*.

For many interesting details regarding Sleep, Dreaming, Somnambulism, Reverie, Mesmerism, &c., the student is referred to CARPENTER'S Mental Physiology. A medical man ought to be acquainted with what is known of the physiological explanation of these states, so as to be able to dispel superstitious notions, which will hold their ground until knowledge drives them away.

MECHANISM OF THE VOICE.

The voice is produced by the vibrations of the vocal cords of the larynx. Voice is to be distinguished from speech, which is the production of sounds intended to express certain ideas. Most animals have voice, but none have the power of speech in the same sense as man possesses that faculty. With the anatomical arrangements of the organ of voice, the student is presumed to be familiar, and all that will be here attempted is to indicate some of the physiological conditions of voice and of speech.

A.—THE PRODUCTION OF SOUND IN THE LARYNX.

This may be studied in three ways: (1) by the use of artificial contrivances resembling the larynx; (2) by experiments made on the dead larynx; and (3) by observations of the movements of the living larynx, with the aid of the laryngoscope.

1. Anatomical Arrangements.

Voice is produced essentially by the movements of two membranous bands, the true *vocal cords,* between the free edges of which the air is forcibly expelled, and the anatomical arrangements are adapted for tightening or relaxing, and separating or approximating, the vocal cords. For this purpose, the larynx consists of a series of individual portions moveable on each other by means of various muscles. These are: (1) the *crico-thyroids*, by pulling the thyroid cartilage downwards and forwards, tighten the true vocal cords; (2) the *thyro-arytenoids* have the reverse effect; (3) the *lateral crico-arytenoids*, by pulling forwards the outer angles of the arytenoid cartilages, approximate the vocal cords; (4) the *posterior crico-arytenoids*, by pulling backwards the outer angle of the arytenoid cartilages, separate the cords from each other; (5) the *arytenoids* also approximate the cords; and (6) the *aryteno-epiglottideans* lower and approximate the arytenoid cartilages, and so pull the epiglottis downwards as to constrict the upper aperture of the larynx.

2. Physical Conditions.

To excite the vibrations of the vocal cords, it is necessary that the air be expelled from the lungs under a certain pressure; but no accurate estimate has been made of its amount. Feeble phonation may also be produced by inspiration. The *intensity* of the voice will be determined by the

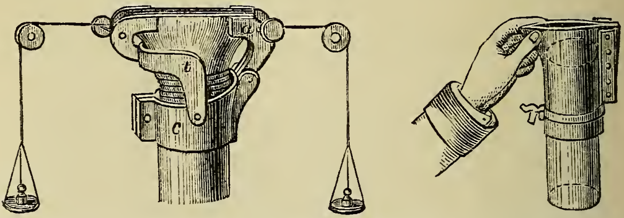


Fig. 187.—To the right, a simple artificial larynx is shown, consisting of a piece of india-rubber tied firmly round the end of a tube. On stretching the upper orifice with the hand and blowing through the tube, sounds of various pitch may be produced. A more complicated apparatus devised by Müller, is shown to the left. *c*, a ring of metal, representing the cricoid cartilage; *t*, a moveable piece of brass, representing the thyroid. The cords, or margins of the india-rubber membrane may be rendered more or less tense by weights.

amount of pressure. The *pitch* of the tone will be determined by the *number* of vibrations of the cords in a given time, a condition depending on the degree of tension of the cords and the width of the aperture between them. To produce tones of high pitch, the edges of the cords are approximated, and they become more tense: the reverse is the case for tones of low pitch. These conditions may be readily studied by means of an artificial larynx, such as is shown in Fig. 187.

3. CONDITION OF THE LARYNX DURING THE EMISSION OF SOUND.

This was first studied by direct inspection by Garcia in 1854, who examined the parts with the aid of the laryngoscope. Since then, many observers, such as Czermak, Wyllie, and Emma Seiler have carefully examined the organ in a similar way. Immediately before emitting a sound, the glottis is closed more or less completely by the approach of the bases of the arytenoid cartilages, and the cords are brought to the requisite degree of tension and length. Then the cords are separated from each other by the air rushing between them, and they are thrown into rapid vibration. The vibrations are transverse to the direction of the cord. Those of the inferior or true cords alone emit only feeble tones; but these are strengthened by the movements of the air in the sonorous tube above the glottis.

4. PHYSIOLOGICAL CHARACTERS OF VOICE.

A tone produced by the human voice resembles any tone produced by a musical instrument, in presenting the characters of intensity, pitch, and quality.

a. *Intensity of Voice.*—As already indicated, this will depend on the amplitude of the movements of the cords; and, consequently, on the force of the current of air expired.

b. *Pitch of Voice.*—This depends on the number of vibrations per second. The length, size, and degree of tension of the vocal cords influence the number of vibrations. The more tense the cords, the higher will be the pitch; again, the greater the length of the cords, the lower will be the pitch. The length of the trachea and of the passages above the cords has no influence on pitch. The range of the human voice is about three octaves, that is, from fa_1 (174 vibs. per second), to sol_4 (1,566 vibs.) In men, by the development of the larynx, the cords become more elongated than in women, in the ratio of 3 : 2, so that the male voice is stronger, and of lower pitch. At the age of puberty, the voice of a boy "breaks," in consequence of the lengthening of the cords, and it generally falls an octave in pitch. The range of the different varieties of voices is shown in Fig. 188.

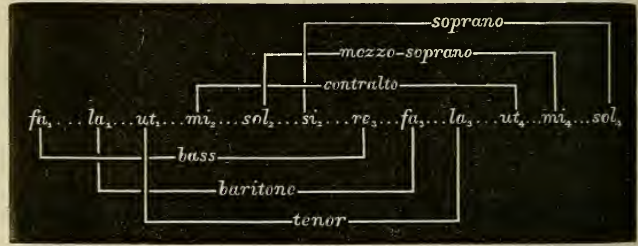


FIG. 188.—Diagram showing the Range of the Human Voice.

There is thus a range for ordinary voices of nearly three octaves, but in some individuals higher or lower tones may be taken; so that three and a half octaves may be fixed as the extreme range. Few single voices have such a range. A basso named Forster had a compass of three octaves, and he could take the note $la_{-1} = 108$ vibrations per second. Catalini commanded three and a half octaves. It is said that the highest observed pitch is given by Nilsson, in *Il Flauto Magico,* as $fa_5 = 2{,}784$ vibrations. The most remarkable voice, however, recorded in the history of vocalization is that of an Italian singer, Lucrezia Ajugari called the *Bastardella,* heard by Mozart in Parma in 1770. Her range was from $sol_2 = 391$ vibrations, to $ut_6 = 4{,}176$ vibrations.

Three varieties of voice are well known: chest notes, falsetto notes, and head notes. The deepest notes are apparently from the chest, the highest from the head, and intermediate notes may belong to both registers, constituting a *mixed* voice. It is a great art in singing to pass gradually from the one register to the other. As the result of her observations, Madame Seiler makes the following statements: “There are five different actions of the vocal organ: (1) “The *first series of tones of the chest-register,* in which the “whole glottis is moved by large, loose vibrations, and the “arytenoid cartilages with the vocal ligaments are in action; “(2) The *second series of the chest-register,* when the vocal “ligaments alone act, and are likewise moved by large, “loose vibrations, as in Fig. “189; (3) The *first series of* “*the falsetto-register,* where, “again, the whole glottis, con- “sisting of the arytenoid car- “tilages and vocal ligaments, “is in action,—the very fine “interior edges of the liga- “ments, however, being alone “in vibration; (4) The *second* “*series of the falsetto-register,* the tones of which are “generated by the vibrations of the edges alone of the vocal “ligaments; and (5) The *head-register,* in which the cords

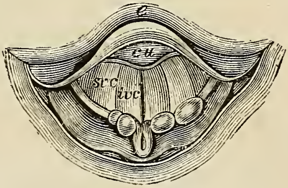


FIG. 189.—The glottis during the emission of a high tone. *c a,* epiglottis; *i v c,* inferior vocal cord; *s v c,* superior vocal cord.

"actually touch, or even overlap to a certain extent, leaving "only a small aperture between the margins of the anterior "third of the cords." (*Seiler's Voice in Singing*, p. 65.)

c. *Quality of Voice.*—This, as is the case with any compound musical tone, depends on the number and the intensity of the harmonics. In many voices, the first five or six harmonics may be detected with resonators. One or more of these may be so strengthened by the resonance of the cavities above the glottis as to give the voice a special quality, as may be proved by singing a tone of the same pitch with the oral cavity in different conditions.

B.—CHARACTERS OF SPEECH.

Speech is composed of articulate sounds produced by movements of the parts forming the pharyngeal and oral cavities and movements of the tongue. *Whispering* is speech without voice; singing a tone without any articulate expression combined with it, is voice without speech. Simple articulate sounds may be divided into vowels and consonants. Compound sounds constitute words.

1. Physiological Characters of Vowels.

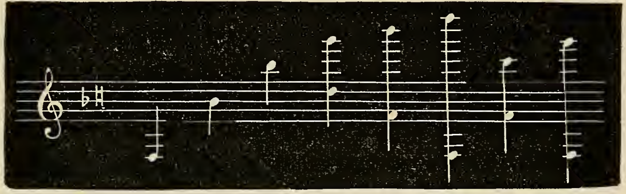
Vowels are musical tones formed in the larynx, some of the partials of which are strengthened by the resonance of the air in the pharyngeal and oral cavities. According to Helmholtz, the buccal cavity is a resonator tuned to a particular tone, depending on its form. This may be proved by putting the mouth in a certain form, keeping the lips open, and bringing various tuning forks sounding feebly in front of the opening. When a fork is found to which the resonant cavity of the mouth corresponds, then it sounds out with considerably intensity. By thus putting the mouth in the position assumed in pronouncing the vowels, the pitch of these may be determined. The following figure shows the pitch of the vowel-tones, according to Helmholtz. More recently, König has reinvestigated the subject, and he has fixed the pitch of the vowels A, E, I, O, OU, as follows :—

Vowels,	OU	O	A	AI	E	I	EU	U
Tone,	fa_2	$si\flat_3$	$si\flat_4$	sol_5	$si\flat_5$	re_6	$ut\sharp_5$	sol_5
				re_4	fa_3	fa_2	fa_3	fa_2

FIG. 190.—Pitch of the vowels, according to Helmholtz.

Vowels,	OU	O	A	E	I
Tones,	$si\flat_2$	$si\flat_3$	$si\flat_4$	$si\flat_5$	$si\flat_6$
No. of Vibs.,	470,	940,	1880,	3760,	7520.

FIG. 191.—Pitch of the vowels, according to König.

If König's observations be correct, it is remarkable that, to produce successively the five vowels, in the above order, the proper tone of the oral cavity showed a rise of an octave from one vowel to another. Calling OU = 1, the values of the other tones will be O = 2, A = 4, E = 8, and I = 16.

The quality of vowel tones may be beautifully illustrated by the aid of an apparatus devised by König, shown in Fig. 192.

It consists of a little capsule *d*, divided by a thin india-rubber membrane. On one side of the membrane there is gas, led out to a small burner, and on the other there is a wide tube, terminating in a mouthpiece. On speaking or singing the vowels into the latter, a characteristic flame-picture will be obtained for each vowel, and even for the same vowel at a different pitch. The flame-picture of a pure tone would consist of equal segments, whilst two or more tones acting on the *same* flame would produce an irregular picture. This may be illustrated by causing two organ pipes, with the apparatus shown in Fig. 183, to act on the

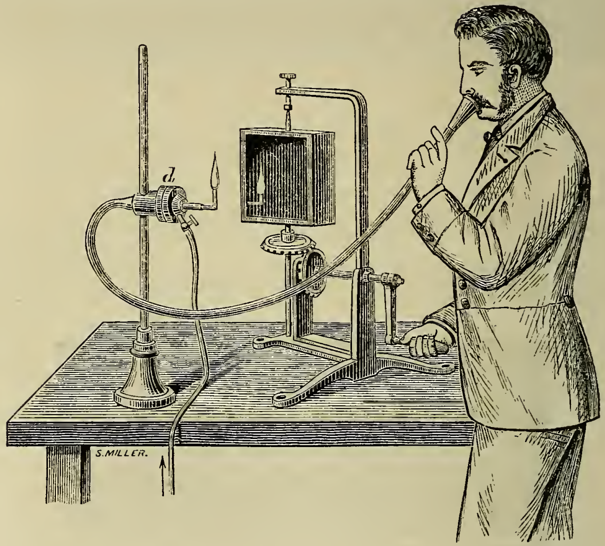


FIG. 192.—König's apparatus for illustrating the quality of vowel tones by a manometric flame.

same flame. The following diagram shows the form of the flames which characterize the vowels A, O, OU, sung at the pitch of ut_1, sol_1, ut_2. Thus the harmonics produced in the larynx are strengthened or reinforced by the proper tone of the oral cavity for a particular vowel; and, consequently, quality of vowel-sound depends chiefly on the form of the oral cavity.

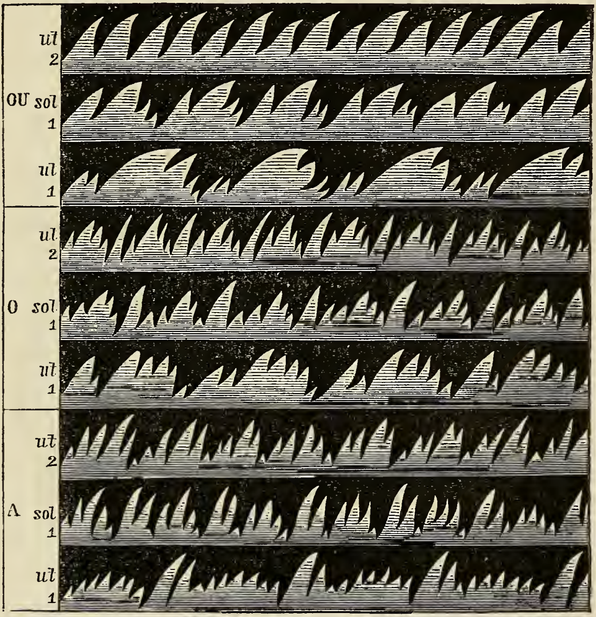


FIG. 193.—Flame pictures of the vowels OU, O, and A, showing their different quality. (*König.*)

2. PHYSIOLOGICAL CHARACTERS OF CONSONANTS.

Consonants are sounds formed in the buccal cavity, and strengthened by the laryngeal sound. There appear to be three special regions of articulation: (1) *Guttural*, from the neighbourhood of the soft palate and base of the tongue; (2) *Lingual*, from the neighbourhood of the superior dental arch, the anterior part of the hard palate, and the tongue; and (3) *Labial*, from the lips. The different consonant sounds may be produced as follows: (1) The oral tube is contracted in the guttural, lingual, or labial regions, and at the same time the air is expelled—thus, *gutturals*, Ch and J; *linguals*, S, Sch; and *labials*, V and F; (2) There is complete and instantaneous closure in the region of articulation, the sound being produced either before the moment of closure, as *a*B, or at the moment of opening, B*a*—such are *gutturals*, G, K; *linguals*, D, T; and *labials*, B, P; (3) There is a kind of vibratory movement given to the articulating region, such as the guttural, lingual, or labial R; and (4) The consonant sound acquires a *nasal* quality, from part of the air passing into the nasal passages, which it does not do in the three preceding cases—such are the *guttural* nasal sounds NG, the *lingual* N, and the *labial* M. These facts are shortly classified in the following table (*Beaunis*):—

Varieties of Consonants.			Regions of Articulation.		
			Labials.	Linguals.	Gutturals.
Continuous,	Hard,		F	S	Ch
	Soft,		V W	Sch Z	J
Explosives,	Simples,	Hard,	P	T	K
		Soft,	B	D	G
	Aspirates,	Hard,	PH	TH	KH
		Soft,	BH	DH	GH
Thrilling,			R	R	R
Nasal,			M	N	NG

The student may consult, regarding voice, Müller's Physiology, translated by Baly, vol. II., p. 1002; Willis, Transactions of the Philosophical Society of Cambridge, 1832; Garcia, Mémoire sur la Voix Humain, 1847; Czermak, Du Laryngoscope, 1860; Helmholtz, Théorie Physiologique de la Musique, 1874, translated by Gueroult; The Voice in Singing, by Emma Seiler, Philadelphia, 1874; and Gavarret, Phenomènés Physiques de la Phonation et de l'Audition, Paris, 1877. Regarding the formation of vowel and consonant sounds, Max Müller's Lectures on the Science of Language.

MECHANISM OF THE ATTITUDES AND THE MOVEMENTS OF MAN.

A.—MECHANISM OF THE BODY IN A STATE OF REST.

The skeleton constitutes a firm, partly rigid and partly moveable framework of support, suitable for posture and locomotion in the erect position. The different bones, more especially those of the limbs, are moved by the muscles in directions determined by the form of the joints and the points of insertion of the muscles.

The term *posture* is applied to those states of equilibrium of the body which may be maintained for a certain time without displacement, such as standing, sitting, or lying. The essential condition of stability is, that the centre of gravity of the body fall within the basis of support. The *centre of gravity*, in the prime of life, is about 4½ inches above the middle distance, or, in the sacro-lumbar articulation, 3½ lines above the promontory of the sacrum. The basis of support is contained in the erect posture between the feet, and will vary according to the distance separating the feet. When the basis is limited to one foot, or to the point of one foot, there is of course a diminution in the equilibrium, so that the slightest oscillation of the line of gravity outside of the basis may cause a fall. To secure the line of gravity falling within the basis, muscular action may be necessary, as in crouching, but fatigue soon supervenes. In the erect posture, however, the anatomical arrangements are such as to ensure stability to a large extent by the action of gravity. Thus, the head is in equilibrium upon the atlas, the centre of gravity falling a little in front of the axis of rotation of the occipito-atloid articulation, muscular action being necessary only to a small extent. The muscles of the back assist in maintaining the straightness of the spine. The centre of gravity of the trunk passes behind the axis of rotation of the femurs, but the body is kept from falling backwards by the tension of the structures in front of the thigh and hip-joint. In the erect posture, all the body, from the tibio-tarsal articulation upwards, forms a more or less rigid structure. It may be observed that the slightest movement at the articulation causes a considerable oscillation of the head and upper parts of the body; and even when the body appears to be quite steady, minute oscillations, of which the individual is unconscious, may be traced graphically. There would thus appear to be a series of limited muscular contractions, now in front, now behind, on the one side or the other, by which the body is so steadied as to prevent the risk of the line of gravity falling outside the base of support. These muscular movements probably contribute to the production of the muscular sense already described, by means of which guiding sensations precede and are related to our movements. (See page 636.)

B.—MECHANISM OF THE MUSCLES.

1. General Mechanism.

In the human body, there are observed different modes of adaptation of the muscles to the bones, corresponding with the three varieties of lever movement. Here the moveable bone represents a lever of which the *fulcrum* is the articulation with the fixed bone, the *power* is employed at the point of insertion of the contracting muscle, and the *resistance* may be of various kinds, according to the obstacles which tend to prevent displacement of the moveable bone.

(1) *Levers of the First Order.*—Here we find the fulcrum between the power and the resistance. As an example, take the balancing of the head on the vertebral column: the fulcrum is the articulation between the occipital bone and the atlas; the resistance is the weight of that part of the head and face in front of the articulation, and the power is behind at the point of insertion of the muscles of the neck. The construction of the vertebral column, the balancing of the trunk on the pelvis, and of the leg on the foot, represent levers of the same kind. Usually, in man, this kind of lever is for the purpose of *stability*, but we find it also in certain movements. For example, in extending the fore-arm upon the arm—the fulcrum is the elbow-joint, the power, applied behind the articulation, is the insertion of the triceps, and the resistance is the weight of the fore-arm in front of the articulation.

(2) *Levers of the Second Order.*—Here the resistance is between the power and the fulcrum. In this lever, the power-arm[1] is always longer than the resistance-arm. As the forces are inversely proportional to the length of the arms of the lever, a comparatively weak force will overcome considerable resistance, and consequently this lever is advantageous as regards expenditure of force. But it is disadvantageous as regards rapidity of movement, for the displacements of the two points of application are proportional to

---

[1] The term *arms of the lever* is the distance which separates the fulcrum from the point of application of the power or of the resistance. The one may be called the *power-arm* and the other the *resistance-arm.*

the lengths of the arms of the lever. For example, if the length of the power-arm = 10, and that of the resistance-arm = 1, a force of 1 lb. would move a resistance of 10 lbs., but the point of application of the power would be displaced 10 feet, while that of the resistance would be displaced only 1 foot. This lever may be termed the lever of *power*. It is not common in the body. As an example, take the action of standing on tiptoe. Here the fulcrum is the contact of the toes with the ground; the power is at the insertion of the tendo Achillis, the strong ligament fixed into the *os calcis*, or heel-bone; and the resistance is the weight of the body transmitted to the articulation between the tibia and astragalus.

(3) *Levers of the Third Order.*—The power is between the resistance and the fulcrum. In this lever, the resistance-arm is always longer than the power-arm, and while it is advantageous as regards swiftness, it is disadvantageous as regards expenditure of force. It may be termed the lever of *rapidity*. It is the one common in the movements of man. For instance, in the flexion of the fore-arm upon the arm—the fulcrum is the articulation at the elbow, the power is at the insertion of the flexors (*brachialis anticus* and *biceps*), and the resistance is the weight of the fore-arm. The power is usually applied in the body near the fulcrum, and the power-arm is thus much shorter than the resistance-arm, and hence only small weights can be moved, but with great speed. Thus the various movements of the body are rapidly performed, and the clumsy form of the limb, which would have resulted had the power been applied near the resistance, is obviated.

Simple movements such as are above described rarely take place. Usually the movements which one bone makes on another are not effected by one muscle, but by several, which may be regarded as associated together for that movement.

Thus, in moving the arm, say from pronation to supination, with a slight degree of flexion or extension, many muscles act.

In many instances, considerable loss of power is caused by the oblique direction in which the tendons of muscles are inserted into the bones, by the combination of several muscles acting in different directions, and by the obliquity of the direction of the fibres in individual muscles. The degree of the obliquity of attachment is, in a number of bones, diminished by the enlargement of their heads, the existence of projecting parts, and still more by the occurrence of sesamoid bones and pulleys, changing the direction of tendons; but, nevertheless, the adaptation of the muscles to the bones, in the human body generally, may be regarded as attended with considerable loss of power; some part of which loss, however, is compensated by greater extent and velocity of motion.

2. The Mechanical Work of Man.

It is almost impossible to calculate the force of a particular muscle or group of muscles in a living man. By means of Regnier's dynamometer, it has been ascertained that the force exerted by the muscles of the back amounts in most adults to from 400 to 600 lbs., and in very powerful adults to 700 or 800 lbs. lifted a few inches. The muscles of the leg exert a power equal to about 400 lbs. As pointed out by Allen Thomson, in calculating the capacity of man or animals for labour, it is necessary to take into account (1) the force of the muscles; (2) the velocity of the motion; and (3) the length of time during which the action is sustained. Thus the horizontal draught power of a horse may be, say 100 lbs. when walking, but if running, as in pulling a conveyance, it may be diminished by one half. If the velocity be doubled, the length of time during which the exertion can be maintained is reduced by one fourth. A porter may carry 200 to 300 lbs. for a short time, at the rate of three miles an hour; but for a day's work, 100 lbs. is quite sufficient. (*Thomson's " Outlines,"* p. 134.)

The age, stature, and weight of individuals modifiy greatly the amount of muscular exertion of which they are capable. The average height of men in Great Britain is about 69 inches, and of women 63½ to 64 inches. With this stature, men weigh from 140 to 160 lbs., women, 110 to 120. The full stature and strength of the male is reached about the age of 25. At 15 years of age, lads, 5 feet 4 inches in height, may lift from 200 to 280 lbs.; at 20, when 5 feet 8 inches in height, the lift is from 350 to 415 lbs.; and at 25, the stature being 5 feet 9 inches, it may reach as much as from 400 to 450 lbs. (*Allen Thomson.*) The following table shows a comparison between the working power of man and of certain animals :—

	Mean Weight.	Work in 8 hours.	Work per second and per Kilogramme of Weight.
	Kilograms.	Kilogrammetres.[1]	Kilogrammetres.[1]
Man	70	316,800	0·157
Ox	280	1,382,400	0·172
Horse	280	2,102,400	0·261

C.—MECHANISM OF THE BODY IN LOCOMOTION.

The movements of the body as a whole assume various forms, such as walking, running, leaping, swimming, &c. It is not within the scope of this work to do more than

---

[1] A kilogrammetre, or unit of work, is the amount of work necessary to lift one kilogramme one metre high in one second of time.

briefly to allude to some general facts. Although many of the movements were investigated by Borelli, about the year 1680, the brothers Weber were the first to adopt rigorous and precise methods. Recently, the whole subject has been re-investigated by Marey, who has devised many ingenious forms of apparatus on the principle of the registration of transmitted movements. His arrangement consists of a slipper or shoe, having a thick sole, in which there is an air chamber *a*, communicating with a recording tambour by the tube *b*. With each pressure of the sole of the foot against the ground, the air is compressed in this chamber, and this pressure, transmitted to the recording tambour, is registered on a cylinder carried by the operator, as seen in Fig. 195. In addition, a small tambour, fitted for transmitting vertical oscillations, is placed on the top of the head. Three tambours record the movements, one for each foot, and one for the ver-

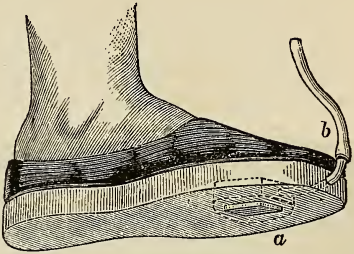


Fig. 194.—Marey's apparatus for transmitting movements from the sole of the foot.

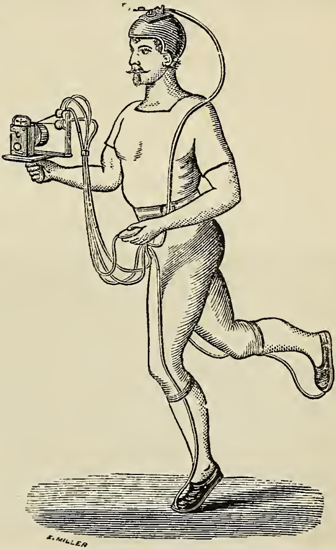


Fig. 195.—Marey's apparatus for recording movement in locomotion.

tical oscillations of the whole body. The operator also is provided with a bag containing air, by the compression of which the three recording levers can be brought against the cylinder when the movements of the body become tolerably uniform. An example of a tracing thus obtained is shown in Fig. 196. Marey has also devised a kind of notation which shows at a glance the rhythm, the time of the duration of the pressure, the foot exerting this pressure, and also the length of time during which the body is suspended. An example showing the mode of this notation is given in Fig. 197. This is the same curve as in Fig. 196,

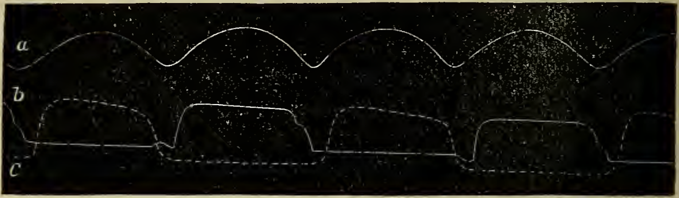


FIG. 196.—Tracings obtained from a man in the act of running. *a*, vertical oscillations of the body; *b*, impact and rise of the right foot; *c*, impact and rise of the left foot. When the foot presses on the ground the curve descends, it remains straight so long as the sole touches the ground, and it ascends as the sole leaves the ground. The upper horizontal part of the curve represents the time the foot remains in the air.

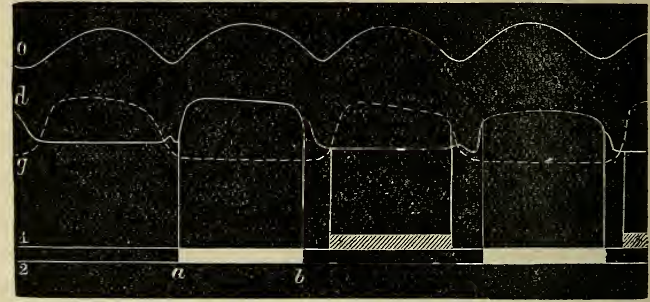


FIG. 197.—Marey's Notation of Rhythm in different modes of progression. Running.

obtained in running. The lines 1 and 2 form a *staff*, "on which will be written this simple music, consisting only of two notes, which we will call right foot, left foot. From the commencement of the ascending part of one step-curve belonging to the right foot, let us drop upon the staff a perpendicular *a*; this line will indicate the commencement of the pressure of the right foot. A perpendicular *b*, let fall from the end of the curve, will determine where the pressure of this foot ends. Between these two points, let us trace a broad white line; it will express by its length the duration of the pressure of the right foot." (*Marey's Animal Mechanism*, p. 133.) A similar construction is made for the left foot. Between the pressure of the two feet there is found to be "*silence*" in the rhythm, that is, the expression of the instant "*when the body is suspended above the ground* in running."

By means of this notation, two of the chief modes of progression are represented in Fig. 198.

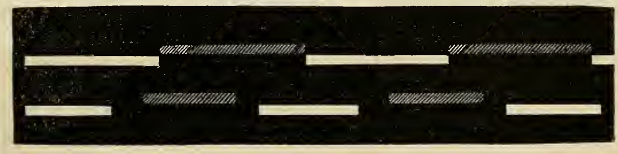


Fig. 198.—Notation of walking (upper line) and running (lower line). (*Marey.*)

1. Walking.

In walking, the body never entirely quits the ground. This is shown by the upper tracing in Fig. 198. The forces which act on the body in ordinary walking may be studied with the aid of Fig. 199. Let G represent the centre of gravity of the body; two forces act on it: (1) the one, represented by the line G J representing the direction of gravity; the other,

(2) produced by extending the limb G J′, causing the centre of gravity to move in the direction G F. The latter may be resolved into two, the one vertical, G V, tending to carry the centre of gravity upwards, causing the *vertical* oscillation in walking; the other, *horizontal*, G H, which determines progression. The two limbs represent a triangle, the hypothenuse of which is formed by the posterior extended limb, the perpendicular G J, on the one side by the limb which supports the body, and the short side, J′ J, represents the length of the step. (*Beaunis.*)

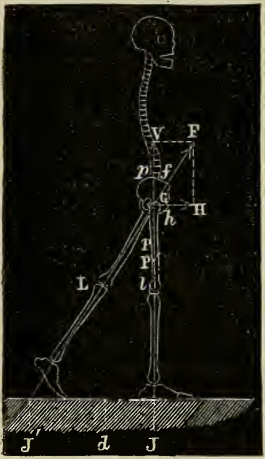


FIG. 199.—Forces which act in walking. (*Weber.*)

At the beginning of the step, one of the limbs, the *active limb*, is placed below the centre of gravity (*p p l*, Fig. 199); and the other, the *oscillating limb* (G J′, Fig. 199) is placed behind. In passing through the complete step, according to Weber, the limbs assume the successive positions shown in Fig. 200.

The advance of the hinder leg itself is not, in ordinary circumstances, as shown by Weber, a muscular action, but consists of the fall or swing of the leg forwards, through the arc of a circle, in a manner similar to the oscillation of a pendulum. It has recently however been demonstrated by Marey and others that frequently, and more especially during fatigue, muscular action is necessary. In quick walking, the advancing leg reaches the ground when only half an oscillation has been performed, but in very slow walking, the limb performs nearly a whole oscillation. The velocity of the advance of the limb is consequently regulated by its length, or by the distance of its centre of gravity from the point of rotation, that is, about 19 inches for a limb of the ordinary length of 34 inches. Increased speed is attained in walking by depression of the centre of gravity of the trunk, greater flexion of the limbs, a more forcible thrust of the hind limb against the ground, longer steps, and by allowing the supporting limb to remain a shorter time in contact with the ground.

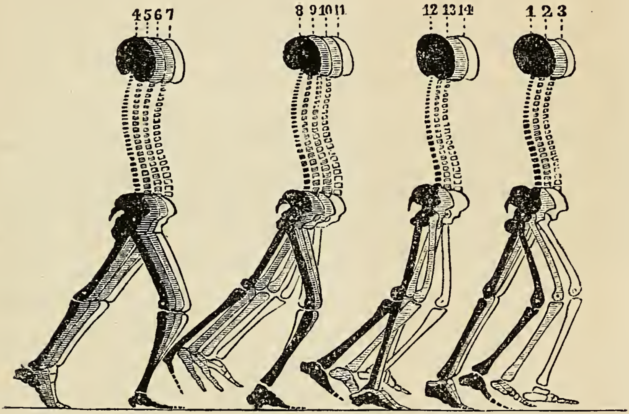


Fig. 200.—Diagram showing the successive positions of the two limbs during walking. (*Weber.*) The positions follow in the order of the numbers.

2. Running.

In running, the hinder leg is raised before the advancing one reaches the ground, so that there is a short time during which the body is not supported by the limbs, as shown in Fig. 198. The trunk is more inclined forwards, the limbs are more bent, the steps longer, and succeed each other more rapidly, and the vertical oscillations are greater than in walking. Thus, the length of the step in running is to that in walking as 2 : 1, and the time as 2 : 3; so that a person may run three times as fast as he can walk. (*Allen Thomson.*)

These movements may also be remembered by the following notation, in which R = right leg, L = left leg, S = supporting, and O = oscillating positions of the limbs:—

Slow Walking,	R—S O S S S S O S S
	L—S S S O S S S O
Quick Walking,	R—S O S O S O
	L—O S O S O S
Running,	R—S O O O S O O O
	L—O O S O O O S O
Jumping,	R—S O S O
	L—S O S O

Consult regarding Animal Locomotion, BORELLI De motu animalium, 1680; E. WEBER, Mécanique de la Locomotion, dans Encyclopédie Anatomique, 1833; BISHOP's Article "Motion" in the Cyclop. of Anat. Physiol.; MAREY's Animal Mechanism, 1874; and PETTIGREW's Animal Locomotion, 1874.

ANIMAL HEAT.

A.—GENERAL CONSIDERATIONS.

All living organisms may be separated, as regards temperature, into two classes: (1) *Warm-blooded*, or those having an almost constant temperature; and (2) *Cold-blooded*, or those whose temperature varies through wide limits with that of surrounding media. The former include mammals and birds, the latter reptiles, amphibians, and fishes. As regards invertebrate animals, our knowledge of the temperature of individuals is limited and untrustworthy.

The temperature of man in the axilla is between 36°·6 and 37°·4 C.; the oscillations, in a state of health, being included in the compass of ·5 of a degree. The temperature of organs is higher than that of the surface of the body; thus, Bernard found 40·6°C. registered in the brain, liver, glands, lungs, and muscles. The blood passing through the right side of the heart is a little warmer than that returned from the lungs, a fact which has been explained by supposing (1) that the blood coming from the liver may be warmer than that of ordinary systemic venous blood, and (2) that the blood is cooled during its passage through the lungs. As the blood passes from the heart, it loses heat. The temperature of venous blood is high or low according to the organ from which it is returned. Thus, while the temperature of the blood in superficial veins is lower than that of corresponding arteries, on the other hand, venous blood returned from muscles and glands is warmer than the arterial blood entering these.

Temperature is increased in various states of disease, a fact now recognized as of high clinical importance. To understand its significance, we must study (1) the production of heat in the body; (2) the relation between heat and mechanical work in a living organism; (3) the distribution and loss of heat; and (4) the arrangements by which the gain and the loss, in a warm-blooded animal, are kept in a state of equilibrium, so that a uniform temperature is maintained in different thermal circumstances.

B.—THE PRODUCTION OF HEAT IN THE LIVING BODY.

Heat is produced in the living body by chemical and mechanical actions.

1. Chemical Actions.

As has been frequently pointed out, most of the operations occurring in the tissues involve chemical changes, principally those of oxidation. Such changes cause the liberation of heat, and it is important to observe that any given oxidation will produce the same amount of heat. Thus, if we oxidize 1 gramme of hydrogen, a given amount of heat will be produced. Even supposing the element exist in a chemical compound, the amount of heat produced by its oxidation will be the same as if it were free. Consequently, the quantity of heat evolved by the oxidation of a complex substance may be ascertained experimentally. The following figures show the approximate number of calories[1] produced by the combustion of 1 gramme of the following substances:—

Hydrogen, .	34	Methylic Alcohol,	5	Albumen, .	5
Carbon, . .	8	Urea, ...	2	Fat, . . .	9

---

[1] A unit of heat, devised by physicists, is called a *calorie.* It is the amount of heat required to elevate the temperature of 1 kilogramme of water from 0 to 1° C.

It will be observed that a given weight of complex organic substances yields less heat than an equal weight of the simple elements, a fact explained by remembering that in the combustion of compounds *complete* oxidation may not take place.

Every chemical change therefore which occurs in the body, whether it be oxidation, hydration, or decomposition, results in the production of heat.

2. Mechanical Actions.

All frictional movements, such as that of the blood in the vessels, the movements of the muscles, the contact of articular surfaces and of tendons, produce heat; but it is impossible to estimate the amount generated by these different causes.

3. The Localities where Heat is produced.

The organs in which the largest amount of heat is liberated are the muscles. This is indicated by the activity of chemical changes occurring in these, by the fact that an increase of temperature may be detected directly, and by the blood returning from a muscle being warmer than that going to it. The muscles, however, are not the only producers of heat, inasmuch as chemical activity manifested in nervous centres, and in the liver and other glands must produce a certain amount. The theory, first put forth by Lavoisier, that heat is produced in the lungs, must be modified to the extent that the amount of heat so produced is more than compensated by the loss due to the passage of carbonic acid in venous blood from the soluble into the gaseous state.

4. Amount of Heat produced by the Living Body.

This is measured by a process termed *calorimetry*, first practised by Lavoisier. His apparatus, as modified by Dulong, is seen in Fig. 112, p. 385. In this experiment, the animal is placed in a metallic box, the air of which is supplied by a gasometer, whilst the vitiated air is drawn away. The box is plunged into a space filled with water or ice, and the whole apparatus is so surrounded by bad conductors of heat as to render the influence of external media as small as possible. The temperatures of the animal and of the water in the calorimeter are taken at the beginning of the experiment. After the animal has remained in the chamber for some hours, the temperatures are again taken, when either of the two following cases may be the result: (1) there is no change in the temperature of the animal at the end of the experiment; or (2) the temperature of the animal is different from what it was at the beginning. In the first case, it is evident that the quantity of heat produced by the animal must have been equal to the quantity of heat given up to the calorimeter, and in the second, supposing the final temperature to be less, the amount of heat lost may be found by subtracting from the number of units of heat gained by the calorimeter the number of heat-units lost by the body of the animal during the experiment, which will be found by multiplying the weight of the animal by its specific heat, and by the number of degrees lost during the experiment. If on the other hand the final temperature be greater, the two quantities must be added to each other instead of subtracted.

By experiments of a similar nature, Hirn has calculated the number of heat-units produced during repose and during work. The average number during 24 hours in a state of repose, is 2,700 calories, which gives about 112 calories per hour. During active work, the amount is considerably increased, as may be shown by the following table:—

	Day of rest.		Day of work.		
	Rest. 16 hrs.	Sleep. 8 hrs.	Rest. 8 hrs.	Work. 8 hrs.	Sleep. 8 hrs.
Number of heat-units produced.	2470·4	320	1235·2	216·96	320
Total,	2790·4		3724·8		

Helmholtz has calculated that during 8 hours of sleep, about 40 heat-units or calories per hour are produced by a man of average size. The above table shows very clearly the increased production of heat by work.

C.—THE RELATION BETWEEN HEAT AND MECHANICAL WORK.

In contrasting the energy of heat and work, it is important to remember that the heat-unit may be transmuted into the work-unit by multiplying by 425, and that the reverse is accomplished by dividing by the same number, that is, a weight of a kilogramme falling one metre in height in one second will produce the same amount of heat as will raise one kilo. of water from 0° to 1° Cent. in one second (see page 6).

During sleep, the principal mechanical activities in operation are the contractions of the heart and of the inspiratory muscles. As stated at page 326, the total cardiac work in twenty-four hours may be valued in round numbers at 60,000 kilogrammetres. The work of the respiratory muscles is about 14,000 kilogrammetres in the same time. Together, these amount to 74,000 kilogrammetres. During eight hours of sleep, we may estimate $\frac{1}{3}$ of 70,000 or about 23,000 kilogrammetres, as representing the internal work of the body. This figure divided by 425 gives nearly 52 calories in the same time. But it has been seen that during sleep about 320 calories are produced, so that, then, in the operations of the living body, from $\frac{1}{5}$ to $\frac{1}{6}$ of the total energy appears as mechanical work. Again, in a day of work, to the 74,000 kilogrammetres representing the work of the heart and respiratory muscles, we add 213,344 kilogrammetres produced by eight hours' work (26,688—the energy in kilogrammetres appearing as mechanical work in one hour—

× 8 = 213,344, the figures given by Hirn); we have then 287,344. This divided by 425 gives about 676 calories, as representing in heat-units the amount of energy expended in the internal work of the body, plus the external work done in eight hours. As seen in the above table, however, during a day of work, 3,724 calories are produced as heat; to obtain the total amount of energy expended in twenty-four hours, we must add to this sum 676 calories, representing in heat-units the mechanical work done by the body during eight hours of work. Together, they amount to 4,400 calories, the total energy of the body during twenty-four hours, eight of which were occupied in mechanical work. It will be observed that about $\frac{1}{6}$ part of the total energy appears as mechanical work. The superiority of the human body, as an apparatus for the utilization of energy, becomes more apparent when we compare the amount of heat formed *during eight hours of work*, and the amount of mechanical work expressed as heat. In these circumstances, it will be found that about $\frac{1}{4}$ or 25 per cent. of the total energy appears as mechanical work, nearly three times that of the best constructed steam engine, which yields only from 8 to 10 per cent.

D.—THE DISTRIBUTION AND LOSS OF HEAT.

The heat produced in various organs and tissues is *distributed* partly by conduction and partly by the agency of the circulating blood. The vessels containing warm blood may be regarded as a system for the equable distribution of heat, so as to produce a more or less uniform temperature. The temperature of any particular part will depend on (1) the absolute amount of heat produced in the organ or tissue; (2) the temperatures of neighbouring organs or tissues and the conductivity, as regards heat, of the tissues between them; (3) the heat given up to the blood as it passes through the vessels; and (4) the heat given up in the case of a superficial organ, such as the skin, to the surrounding medium.

Heat is lost from the body either (1) by radiation from the cutaneous surface; (2) by heating the air of inspiration; (3) by heating cold foods or drinks introduced into the alimentary canal; and (4) by becoming *latent*, in the evaporation of water from the surface of the skin. It has been estimated that of 100 calories of heat, 87·5 are lost by the skin (73 by radiation and 14·5 by evaporation); 10·7 by the lungs (7·2 by evaporation, and 3·5 by heating of the air inspired); and 1·8 by heating of the ingesta. It will be observed how large a part of the percentage (nearly 90 per cent.) is accounted for by the skin, showing the importance of this organ as a regulator of heat. Its activity depends largely on the temperature and on the hygrometric state of the atmosphere, behaving precisely like any evaporating surface. The *movement* of the air is of great importance. When layers of the air in contact with the surface of the body are renewed at frequent intervals, the skin loses heat at each instant both by radiation and evaporation; so that by keeping a layer of air next the body by means of clothing, the cooling of the body is more slowly accomplished. This result is still further effected by wearing articles of clothing which are bad conductors of heat.

E.—EQUILIBRIUM BETWEEN LOSS AND GAIN OF HEAT.

The maintenance of a uniform temperature is essential to the life of a warm-blooded animal. To maintain it, it is evident that there must be arrangements by which the production and the loss are balanced. These have been well summarized by Beaunis as follows:—

1. The temperature may *increase*—

a. By an increased production, the loss not changing.
b. By a diminution in the loss, the production not changing.
c. By an increased production and diminished loss.
d. By an increased production and insufficient increase in loss.
e. By a diminished amount of loss along with a diminished production, if the first be in excess of the second.

2. The temperature may *diminish* in the contrary cases.

To put the matter still more shortly:—

1. The *production* of heat must increase, if an equal temperature is to be maintained, when

a. There is an increased mean temperature, the loss not varying.
b. The mean temperature is kept constant, although the loss increases.
c. With a fall of mean temperature, if the loss be very considerable.

2. The *loss* of heat must increase, if an equal temperature is to be maintained, when

a. There is a diminution of mean temperature, if the production of heat does not increase.
b. When a mean temperature is maintained, the production of heat being increased.
c. When there is an increase of mean temperature, the production of heat being greater.

These phenomena are chiefly regulated by the relative activities of the skin and of the circulation. If the skin of a warm-blooded animal be coated over its whole extent with an impermeable varnish, it will soon die, after difficulty in breathing, diminished and frequent pulse, *a fall of temperature* from 40° C. to 19° or 20° C., and albuminous urine. It is impossible at present satisfactorily to explain all of these effects; the most probable theory being that such a coating may cause vascular paralysis of internal organs, on the actions of which the production of heat largely depends.

The influence of the nervous system on heat is still obscure. As explained, in treating of the sympathetic nerve, section of the nerve causes increased temperature on the affected side. This effect has been explained chiefly by the increased afflux of warm blood from the dilated state of the vessels. Section of the cord causes a fall of temperature which may be accounted for by dilatation of vessels throughout the body, causing an increased loss of heat by radiation and conduction, because it has been ascertained that if the animal be kept in a warm chamber, the temperature increases instead of diminishes.

Consult regarding animal heat, LAVOISIER, Essai sur la Respiration des Animaux, 1777; DAVY, An Account of some Experiments on Animal Heat, Phil. Trans. 1814; Observations on the Temperature of Man and Animals, Edinburgh Med. Jour., 1826; DESPRETZ, Recherches expérimentales sur les Causes de la Chaleur animale, Annales de Chimie et de Physique, 1824; HIRN, Recherches sur l'Équivalent mécanique de la Chaleur, 1858; HEIDENHAIN, Mechanische Leistung. Wärmtwicklung und Stoffumsatz bei der Muskelthätigkeit, 1864; WUNDERLICH, On the Temperature of the Body in Disease, 1877; CLAUDE BERNARD, La Chaleur animale, 1872; also, a paper by JAMES FINLAYSON, on some indications of a Daily Periodicity in the Vital Functions of Man, read before the Philosophical Society of Glasgow, Dec. 3rd, 1873.

REPRODUCTION.

A.—GENERAL STATEMENT.

Living organisms possess the power of reproducing their kind. The process by which they do so may be either a-sexual or sexual. Some physiologists assert a third mode of reproduction, often termed spontaneous generation, that is, the origin of living beings *de novo*, without parents.

1. SPONTANEOUS GENERATION.

It is beyond the province of this work to enter upon the vexed question of the possibility of the origination of life from dead matter, without the existence of parentage.[1] In the opinion of the author, no definite instance of life originating *de novo* has been proved, whilst, on the other hand, numerous experiments appear to negative its possibility. There can be no doubt that the rigid exclusion of air from boiled infusions of organic matter does prevent the occurrence of life in these infusions. Nor can there be any doubt that in water and in air there are innumerable living particles, termed germs, which, when they fall into a fluid having organic matter in solution, multiply therein, and so excite fermentive or putrefactive changes. The admission of these facts, however, does not appear to invalidate the

---

[1] Such a mode of production of living things is sometimes termed *abiogenesis* or *heterogenesis.*

possibility of abiogenesis occurring in certain conditions, and it is unphilosophical to assert, as many do, the impossibility of its occurrence now or in some past time. The intimate relations known to exist between physical, chemical, and vital phenomena, depending on the laws of the conservation and transmutation of energy, and the theory of evolutional development, indicate the probability of abiogenesis, and it is one of the problems of biological science to ascertain the conditions in which this may occur.

The student may consult regarding this matter, PASTEUR, Mémoire sur les Corpuscles organisés qui existent dans l'Atmosphere, Ann. des Sciences Natur., 1861; BASTIAN, Beginnings of Life, 1872. A critical account of the subject by one favouring the view of abiogenesis will be found in BENNETT'S Physiology, p. 421.

2. ASEXUAL GENERATION.

This mode of reproduction, which includes generation by budding, by fission, or by endogenous formation, has been already referred to in treating of cells, at p. 63. A variety of it constitutes *parthenogenesis*, by which we understand the production of offspring, unlike their parents, which may take place without, in connection with each individual birth, a union of male and female elements. This is often termed the law of *alternate generations*, and it is illustrated by the development of various forms of *Medusæ*, *Tænia*, and of *Aphides*. Here one sexual congress is sufficient, not for one, but for several generations of beings, some of whom may have certain characters unlike those of their immediately antecedent parent.

Regarding this subject, consult OWEN on Parthenogenesis, 1849; SIEBOLD on Parthenogenesis, translated by DALLAS, 1857; HARVEY on the Seed and Bud; SPENCER COBBOLD on Entozoa; and AGASSIZ on the Structure of Animal Life. Details will also be found in works on General Biology.

3. SEXUAL GENERATION.

In the higher animals, reproduction essentially is the result of the blending of two elements—a female element, or *ovum*, and a male, or *spermatozoid*. These are differentiated parts of the body of the parent, and by their union activities are initiated which result in the development of a new being. They may be produced in the same individual, as in many mollusca, a condition termed *hermaphroditism;* but in the higher animals, they are to be regarded as specially differentiated products supplied by different individuals.

a. *The Ovum.*

The ovum is a nucleated cell developed in a special organ called the *ovary*. The ovum is formed in a minute sac in the ovary known as a *Graafian vesicle.* The cell wall is called the *vitelline membrane;* the contents, the vitellus or yolk; the nucleus, the *germinal vesicle;* and the nucleolus, the *germinal spot.* Fecundation essentially consists in the entrance into, and fusion with, the ovum of one or more spermatozoids; after which, changes occur which result in a more or less complete segmentation or division into individual portions of the yolk. If this segmentation involve the *whole* ovum, it is termed *holoblastic,* as in mammals, batrachians, lower crustaceans, worms, &c.; but if it involve only a portion of the vitellus or yolk, so as to leave the remainder for nourishment during the early stages of the embryo, it is called *meroblastic,* as occurs in the ova of birds, amphibians, upper crustacea, insects, and cephalopods.

According to Balbiani, in addition to the *germinal vesicle,* sometimes called Purkinje's vesicle, another vesicle is developed from the wall of the Graafian vesicle, which passes into the ovum and there excites changes which may be termed those of *pre-fecundation.*

b. *The Spermatozoids.*

The male element, or spermatozoid, is a minute filament of various form and size in different animals, consisting of a *head* and a filiform appendage or *tail.* While alive, it moves in a fluid by undulations or vibrations of the tail. They exist in large numbers in the *semen,* the secretion of the testicle of a healthy adult animal; and it has been ascertained that they are developed in the interior of cells lining the semeniferous tubules of the testicle.

c. *Special Stages in the Evolution of the Egg.*

These are (1) the formation of the ovum in the Graafian vesicle; (2) the fusion of the embryonic vesicle of Balbiani with the vitellus or yolk; (3) the extrusion of at least a portion of the germinal vesicle of Purkinje, aided by the formation of peculiar transparent globules, called *polar globules,* and by the slow *rotation* of the yolk;[1] (4) fecundation, or the entrance into the ovum of spermatozoids; (5) segmentation, more or less complete of the yolk, which ultimately terminates in the formation of the *blastodermic membrane,* by the development of which the tissues and organs of the future being are formed.

B.—GENERATION AS REGARDS THE PARENTS.

This includes (1) the formation of the male and female reproductive elements; (2) the union of the two (fecundation); (3) the changes consequent thereon in (*a*) the mother, and (*b*) the child.

---

[1] The rotation of the yolk may be seen in the ova of an animal easily obtained, the common *Lymnaea stagnalis,* of our pools. In a small vase of water, it usually soon deposits eggs on the side, and the development of these may be easily studied with a low microscopic power, placed horizontally.

1. THE MALE ELEMENT IN REPRODUCTION.

The testicle is a tubular gland, the structure of which will be readily understood by reference to any anatomical work. In the tubes, cells are developed (probably from the epithelium lining the walls of the tubes), in the interior of which one or more spermatozoids are formed. These cells rupture, the spermatozoids are set free, and mixing with mucus, a fluid is produced termed *semen*. It may be regarded as a special kind of secretion, involving not only chemical but also morphological elements. When *semen* is examined microscopically, it is often found to be teeming with spermatozoids; but occasionally only a few may be present. To watch their movements, it may be necessary to dilute the semen with a drop of water at a temperature of about 98°F. Water above or below this temperature usually stops the movements at once. The movements are due to a kind of wriggling motion of the tail, very similar to those of long cilia, but no actual shortening or lengthening can be seen with the highest microscopic power. By these movements, which, like some other protoplasmic phenomena, may last for some time after the death of the individual, they pass along the female genital passages, so as to meet the ovum. They may be found in the semen of men from eighteen to eighty years of age. The development of spermatozoids seems to be coincident with changes in many bodily organs, more especially in the larynx and in the production of epidermic appendages. This law is prominent throughout the life-history of most vertebrate animals.

2. THE FEMALE ELEMENT IN REPRODUCTION.

The ovum is developed in a special organ, the ovary, consisting of a fibrous and vascular stroma, in which are embedded ova in various stages of development. These are found as small nucleated cells, even in the ovary of a newly born child, and it has been shown, by studying its development from an early stage, that the ovary is really a modified tubular gland, and that the cells, which ultimately become ova, are derived from the peritoneal epithelium. In a young ovary, small follicles or pouches begin to form round the ovum, at first round the periphery of the organ, but ultimately, as they become larger, occupying its deeper parts. These follicles are known as *Graafian Vesicles.* A fully matured vesicle consists of an envelope or wall lined by epithelium, thus forming a layer called the *membrana granulosa.* At one point of the vesicle, usually that opposite to the surface of the ovary, the cells forming this membrane are collected into a mass or disc, the *discus proligerus,* which projects into the interior of the vesicle, and on the surface of which the ovum is situated. Surrounding the ovum, there is a layer of cells, derived from the disc, called the *tunica granulosa.* Between the membrana and tunica granulosa, there is a little fluid matter.

When an ovum and Graafian vesicle have reached maturity —which happens in the human female, in a temperate climate, about fifteen years of age, and, as ova are successively developed, may continue at stated intervals, up to forty-five years of age,—the vesicle bursts, and the ovum is discharged into the dilated end of the Fallopian tube, which is believed to be closely connected with the ovary at that time. The rupture of a vesicle and the discharge of an ovum are accompanied, or are followed, by changes both in the ovary and in the uterus. The changes in the ovary lead to the formation of a *corpus luteum,* and those in the uterus and other parts give rise to the phenomena of menstruation.

a. *Formation of a Corpus Luteum.*

After the rupture of a Graafian vesicle, there is a small effusion of blood which fills up its cavity. This coagulates, and, in course of time, undergoes retrograde changes similar to those occurring in any effused blood. The fluid is reabsorbed, the corpuscles disintegrate, the colouring matter splits up so that crystals of hæmatoidine are produced, and the clot shrinks and becomes of a yellow colour. Coincidently with these changes, there appears to be a hypertrophy of the fibrous wall of the vesicle and of the membrana granulosa, so that the thickened wall follows the retracting blood clot irregularly, and thus a *yellow body*, frequently of a stellate shape, is produced. At this period, the vessels in the neighbourhood of the follicle are large and numerous, but gradually they disappear, with the result that fatty changes occur in the corpus luteum, so that, as time goes on, it becomes less and less marked, and in the ovary of a person in advanced life, may be represented only by a puckered cicatrix.

b. *The Phenomena of Menstruation.*

From the age of fifteen to that of forty-six years, an ovum escapes from the ovary of the healthy human female at intervals of twenty-eight days. This occurrence is coincident with various changes in the uterus and pelvic organs, which cause both local and general symptoms. The local conditions are (1) a somewhat increased size of the uterus, probably from the increased afflux of blood; (2) thickening of the mucous membrane; (3) portions of mucous membrane may become detached; and (4) capillaries are ruptured so as to produce a discharge of blood, mixed with mucus, termed the *menses* or *menstrual fluid.* This discharge continues for a period of from three to five days; sometimes copious, but more frequently scanty at the commencement, it reaches a maximum in amount, and then slowly passes away. Frequently the woman suffers at the menstrual period from a sense of fulness in the pelvic region, weariness, pains in the back and limbs, and other constitutional affections. Menstruation rarely occurs during pregnancy or lactation. Although there is, in a healthy state, an intimate connection between ovulation and menstruation, the latter, or some phenomenon very similar to it, may possibly occur without the former.

c. *Puberty in the Female.*

The age of puberty marks the capability for procreation. In temperate climates, it occurs usually at the age of fifteen or sixteen years. The term of fecundity in healthy individuals is about thirty years, but there are many exceptions to this rule. At puberty, changes occur not only in the generative organs but in other parts of the body, giving to the female form the characteristic appearances of womanhood.

d. *The Change of Life, or Climacteric Period.*

At the age of about forty-five, the menses cease. The change occurs gradually, the amount of fluid becoming less at each successive period; but in some women, there may be intervals of many weeks, or even months, between the last few menstrual periods. A series of bodily changes, the reverse of those occurring at puberty, supervene after the cessation of menstruation.

e. *The Passage of the Ovum to the Uterus.*

When an ovum escapes from a Graafian vesicle, it is received into a space formed by the fimbriated extremity of the Fallopian tube grasping the ovary. The dilated end of the tube appears to be applied to the ovary, probably by a reflex influence exciting the muscular fibres of the dilated end of the tube. In some rare cases, the ovum may drop into the peritoneal cavity, and if fecundation occur in these circumstances, extra-uterine pregnancy will be the result. The ovum is carried along the tube by ciliary movement. It is impossible to state precisely the length of time the ovum will require to pass onwards into the uterus.

3. The Phenomena of Fecundation.

These include two distinct sets of actions: (1) the arrangements by which the fecundating fluid, the semen, is introduced into the generative passages of the female; and (2) the essential act of fecundation, namely, the entrance into the ovum of spermatozoids.

a. *The Preliminary Acts of Fecundation.*

In fishes, the male sprinkles the spermatic fluid over the spawn of the female, and there is no congress of the sexes in any sense. In many amphibians and reptiles, the male clings to the back of the female, and sheds the semen over the ova as they pass from the cloaca or uro-genital aperture. In birds and mammals, the fecundating matter must be introduced by a special organ, the penis, into the generative passages of the female. The penis becomes rigid owing to an increased afflux of blood, due to the action of nervous filaments, which either cause a dilatation of arteries or a diminution in the calibre of the veins of the organ. Goltz has found that a nervous centre connected with erection exists in the lumbar region of the spinal cord. Tactile or psychical influences may excite this centre, which acts through the sacral nerves and hypogastric plexus. In the female, during coition, there are phenomena of a similar kind affecting the clitoris, the vaginal walls, the uterus, and possibly the Fallopian tubes. Coitus results in the ejaculation of semen by a reflex mechanism excited by contact. The semen accumulates in the vesiculæ seminales; by contractions of these vesicles and of their efferent canals, the fluid passes into the urethra, from which it is expelled by rhythmical contractions of the fibres surrounding the bulbous part of the urethra. At the same moment, it is mixed with the secretion of the prostate and of Cowper's glands. It has been supposed that, in the female, a discharge also occurs from Bartholini's glands.

b. *The Essential Act of Fecundation.*

Fecundation consists of the penetration into the ovum of spermatozoids. These disappear in the matter of the ovum, so that the male and the female elements ultimately blend together, thus forming one mass, from which the future being originates.

4. THE CHANGES FOLLOWING FECUNDATION.

These may be conveniently divided into—(1) the changes in the ovum which lead to the formation of an embryo; and (2) the changes in the uterus fitting it for the reception and nourishment of the embryo.

a. *Changes in the Ovum after Fecundation.*

The minute description of the successive changes in the ovum after fecundation now belongs to a department of biological science termed *Embryology*, which has, during the past thirty or fifty years, assumed such proportions, and involves so many points of minute detail, as to place it beyond the province of this work, which treats specially of the functions of the individual after birth.

A full account will be found in the elaborate chapter on

Embryology in Quain's Anatomy, vol. II., pp. 673, written by Dr. Allen Thomson. The following are the chief points to be noticed:—

1. The formation, by repeated fission of the germinal part of the vitellus or yolk, of a stratum of embryonal cells called the *blastoderm,* in which all subsequent development takes place.

2. The separation of the blastoderm at first into two and afterwards into three layers, named respectively the *epiblast,* (outermost), mesoblast (middle), and hypoblast (internal).

3. As regards the body of the embryo itself, its various systems and organs are generically related to these layers thus:—

   a. From the *epiblast,* there are formed the epidermis and its appendages, the cerebro-spinal axis, and the chief parts of the eye, ear, and nose.

   b. From the *hypoblast,* there are formed the epithelial lining of all the alimentary canal, except the mouth, and the epithelial lining of the lungs and ducts of glands.

   c. From the *mesoblast* evolve the skeleton, muscles, fascia, tendons, nerves, true skin, the connective tissues, the vascular system, the blood, the muscular and fibrous coats of the alimentary canal and visceral passages, serous membranes, parenchyma of glands, and the genito-urinary system. (*Allen Thomson.*)

4. The formation of certain sacs and membranes, associated with the nutrition of the early embryo and the mode of its adaptation to the uterus, the cavity specially fitted for its reception. These sacs are the *umbilical sac,* found in all vertebrate animals, and the *amnion* and *allantois,* common to birds and mammals, but absent in amphibia and fishes.

5. The *umbilical sac* or *yolk* sac is a covering developed from the blastoderm, spread over the surface of the yolk

within the vitelline membrane; the *amnion* is a sac, developed partly from the epiblast and partly from the mesoblast which arises as two folds or layers from the cephalic and caudal extremities and from the sides of the embryo. These folds pass backwards, converge over the surface of the embryo, and ultimately coalesce. The outer portion of the fold constitutes for the time an outer covering of the embryo, taking part in the formation of the chorion, and the inner remains near the body of the membrane. The separated inner division, connected with the integument of the body at the umbilicus, forms the sac of the amnion, containing the amniotic fluid. This fluid contains about 1 per cent. of solid matter, consisting of albumen and traces of urea. (*Allen Thomson.*) The *allantois,* or urinary vesicle, is a sac developed in the caudal extremity of the embryo, and may be regarded as originating from the primitive intestine. It soon attains considerable size, and vessels are developed in its outer layer. The allantois is a flask-shaped vesicle, filled with fluid. In birds, it lines the whole of the inner surface of the membrane of the shell, and is thus related on the one side to the air, and on the other side to the albuminous matter.

6. The *chorion* is the name given to a layer or membrane formed around the ovum by the time the latter is placed in that part of the uterus which it is to occupy during intra-uterine life. At an early period, it presents a villous or shaggy appearance, from the development of numerous villi into which vascular loops or tufts are prolonged from the vessels ramifying on the allantois. The ultimate use of these villi is to establish an organic connection between the ovum and the uterus, and consequently they play an important part in the formation of the placenta.

7. As regards the development of special organs and tissues, details will be found in the writing above referred to.

b. *Changes in the Uterus after Fecundation.*

As the ovum descends the Fallopian tube, the uterus is undergoing changes fitting it for that intimate organic union that is to exist for a time between the two. The mucous membrane becomes more vascular, increases in thickness, and bulges into the cavity of the uterus in the form of small irregularly-rounded processes. The uterine glands also increase in size, and pour out a copious secretion. This thickened mucous membrane is called the *decidua vera.* When the ovum passes into the uterus, it becomes entangled in the decidua vera; a fold of decidua, called *decidua reflexa,* is formed around it; and the villi of the chorion, already referred to, are pushed into the follicles of the decidua, so as to bring the blood of the embryo into close relation to that of the mother. The name *decidua serotina* is given to that part of the decidua which exists between the ovum and the wall of the uterus. At first, the ovum is surrounded with vascular decidual membranes, but afterwards the vessels in the decidua reflexa, and those of the chorionic villi related to them, atrophy, whilst those opposite the decidua serotina increase in size. Thus, ultimately, the ovum is connected with the uterus on one side by means of a special organ, the placenta.

There is still considerable difference of opinion among embryologists as to the minute structure of the placenta; but there are a few authentic points of physiological import to be kept in mind:—

1. The placenta essentially consists of a fœtal and a maternal part. The *fœtal* part is formed by the villous tufts of the chorion, containing loops of vessels derived from the allantois. It is connected with the fœtus by the umbilical cord, and both it and the cord are covered by a reflection of the amnion. The *maternal* part consists of the

decidua serotina, or hypertrophied mucous membrane between the ovum and the uterus, containing the uterine follicles. These follicles become enlarged; the tufts of the chorion are pushed into them; and the bloodvessels on the outer aspect of the follicles become dilated into large vascular spaces or *sinuses*. The tufts of the chorion come into close organic connection with the walls of these sinuses, so that the blood of the fœtus is in near proximity to that of the mother, but is separated from it by the following membranes: (1) the wall of the fœtal capillary; (2) the wall of the uterine follicle; and (3) the wall of the uterine sinus. Through these membranes interchanges, both as regards nutritive materials and aëration, occur between the blood of the mother and that of the fœtus.

5. The Phenomena of Pregnancy.

In the human being, the term of pregnancy is from 275 to 280 days (or ten lunar months) from the time of fecundation. During that time, the uterus increases in size, its wall becomes enormously thickened, and the organ rises gradually from the pelvis into the abdominal cavity. Coincident with these changes, the mammary glands increase in size; the areolæ round the nipples become darker in colour; not unfrequently pigment may be deposited in unusual quantity in the skin; the female may become full and plethoric, more especially during the later months, and there are many constitutional effects varying in different individuals.

6. The Phenomena of Parturition.

The fœtus is expelled by the contractile force of the uterine walls, aided by the abdominal and other muscles. It is soon followed by expulsion of the placenta. When the latter separates, in the human female, the uterine vessels are torn across, and there is a loss of blood. The hæmorrhage, which comes chiefly from the large placental sinuses, in a healthy state, is soon arrested by the powerful contractions of the uterus. The whole placenta, maternal and fœtal, separates and is extruded. The inner surface of the uterus, opposite the attachment of the placenta, may be covered with shreds of decidual membrane and clots of blood, both of which are ultimately removed in a discharge, termed the *lochia*, which passes for several days. After parturition, the muscular walls of the uterus atrophy by fatty degeneration, and the mucous membrane resumes its normal state.

There appears to be a reflex centre in the lumbar region of the spinal cord, connected with the rhythmic contractions of the uterus during parturition.

In a healthy woman not supplying her offspring with milk, ovulation and menstruation usually commence about six weeks after the accouchment. If lactation be persevered in, as a rule, menstruation does not occur until after a period of ten or twelve months.

7. The Phenomena of Lactation.

The milk of the mother is secreted by the *mammary glands*. In the human female, they form two rounded masses, placed one on each side of the front of the thorax. They are formed on the racemose type of gland structure, resembling the pancreas and salivary glands, consisting of a number of little lobules, from which fifteen to twenty ducts originate. These ducts converge towards the areola, or circle around the nipple, where they form sinuses. From these sinuses, small ducts pass to the surface of the nipple, on which they open by separate orifices. The secretion of milk begins during the later period of pregnancy, but it is not fairly established until two or three days after parturition. Usually its appearance after delivery is preceded by a state of constitutional disturbance, called milk fever. The fluid first secreted is of a yellow colour, may have a peculiarly strong odour, and is called *colostrum.*

(*a*) *Microscopical Characters of Milk.*—It consists of a fluid in which there are numerous globules of various sizes, varying from the $\frac{1}{2500}$ to $\frac{1}{1500}$th of an inch in diameter. They are often in groups, but in healthy milk they should show no tendency to adhere, but roll freely on each other. Colostrum, in addition, contains large globular and granular corpuscles about the $\frac{1}{1200}$ of an inch in diameter.

(*b*) *Chemical Composition of Milk.*—This will be seen in the following table, compiled from various authorities:—[1]

CONSTITUENTS.	HUMAN.	COW.	ASS.	EWE.	DOG.
Water, . . .	828	870·2	916·5	856·2	—
Sugar, ...	70	47·7	60·8	50·0	20
Casein and Extractives,	40	44·8	18·2	45·0	—
Butter, . . .	50	31·3	1·1	42·0	90
Salts, ...	3.1	6·0	3·4	6·8	12
	1000·0	991·1	1000·0	1000·0	—

As regards the ash, Vernois and Becquerel found in human milk 6·9 per cent. of carbonate of calcium, 70·6 per cent. of phosphate of calcium, 9·8 per cent. of chloride of sodium, 7·4 per cent. of sulphate of sodium, and 5·3 per cent. of other salts.

It will be seen, from the above table, that ewe's milk is the richest of all milks, while the milk of the ass is rich in sugar, but poor in butter and casein. Human milk and cow's milk are, on the whole, much alike, and when the

---

[1] The analyses of human milk is by Simon; of the cow, ass, and ewe, by Chevallier and Henry; and the incomplete analysis of that of the dog by Vernois and Becquerel.

latter is used for infants, the reason for adding a little sugar to it will be at once seen.

C.—CIRCULATION OF THE BLOOD IN THE FŒTUS.

In the mature fœtus, the fluid brought from the placenta by the umbilical vein is partly conveyed at once to the vena cava ascendens, by means of the ductus venosus, and partly flows through two trunks that unite with the portal vein, returning the blood from the intestines, into the substance of the liver, thence to be returned to the vena cava by the hepatic vein. Having thus been transmitted through the two great depurating organs, the placenta and the liver, the blood that enters the vena cava is purely arterial in its character; but, being mixed in the vessels with the venous blood returned from the trunk and lower extremities, it loses this character in some degree by the time that it reaches the heart. In the right auricle, which it then enters, it would also be mixed with the venous blood which is brought down from the head and upper extremities by the descending cava, were it not that a provision exists to impede (if it does not entirely prevent) any further admixture. This consists in the arrangement of the Eustachian valve, which directs the *arterial* current (that flows upwards through the ascending cava) into the *left* side of the heart, through the foramen ovale, whilst it directs the *venous* current (that is being returned by the descending cava) into the *right* ventricle. When the ventricles contract, the arterial blood contained in the left is propelled into the ascending aorta, and supplies the branches that proceed to the head and upper extremities before it undergoes any further admixture; whilst the venous blood contained in the right ventricle is forced into the pulmonary artery, and thence through the ductus arteriosus—branching off from the pulmonary artery before it passes to the two lungs—into the descending aorta, mingling with the arterial currents which that vessel previously conveyed, and thus supplying the trunk and lower extremities with a mixed fluid. A portion of this is conveyed, by the umbilical arteries, to the placenta, in which it undergoes the renovating influence of the maternal blood, and from which it is returned in a state of purity.

In consequence of this arrangement, the head and upper extremities are supplied with pure blood returning from the placenta, whilst the rest of the body receives blood which is partly venous. This is probably the explanation of the fact, that the head and upper extremities are most developed, and from their weight occupy the inferior position in the uterus. At birth, the course of the circulation undergoes changes. As soon as the lungs are distended by the first inspiration, a portion of the blood of the pulmonary artery is diverted into them, and there undergoes aëration; and as this portion increases with the full activity of the lungs, the ductus arteriosus gradually shrinks, and its cavity finally becomes obliterated. At the same time, the foramen ovale is closed by a valvular fold, and thus the direct communication between the two auricles is cut off. When these changes have been accomplished, the circulation, which was before carried on upon the plan of that of the higher reptiles, becomes that of the complete warm-blooded animal; all the blood which has been returned in a venous state to the right side of the heart being transmitted through the lungs before it can reach the left side, or be propelled from its arterial trunks.

Consult regarding many interesting points connected with the phenomena of reproduction in the human being MATTHEWS DUNCAN, on Fertility and Sterility, 1872.

DEATH.

Death is the cessation of all vital phenomena, without the capability of resuscitation. During the whole of the lifetime of an individual, there is death in one sense occurring here and there throughout the body. Each tissue is developed, grows to maturity, performs its functions, decays, and dies. Probably no tissue lasts throughout the whole of the somatic life. Thus the cells of the blood are continually changed. Again hairs, nails, feathers, and teeth have each a certain period of existence, at the termination of which they die and separate from the rest of the body. At last, however, a time comes when the general death of the body takes place. This is what we usually term *death*. It results from failure either of the action of the heart, of the lungs, of the brain, or from death of the blood, as in cases of severe septic poisoning. Death beginning at the heart (*fainting*) is termed *syncope*, at the brain, *coma*, and at the lungs, *asphyxia*. When the action of the heart becomes weaker and weaker until it ceases to beat, either from feebleness of its walls, or from poisoning by carbonic acid or want of oxygen, in consequence of a state of asphyxia, death is said to occur by *asthenia*. After *somatic* death, the tissues may live for a short time, but they gradually die one by one. Muscular irritability disappears, and the muscles stiffen from coagulation of their substance. This state, the "stiffness of death," is called *cadaveric rigidity*. After a time the rigidity passes off, the muscles and other tissues become soft; and the body, subjected to the physical and chemical agencies of nature, is resolved into the elements of which it was at first composed.

Such is the history of human existence according to the light of physiological science. The doctrine of a future life, which has been held more or less distinctly in all ages, and in all states of civilization, rests upon evidence of another kind, regarding the validity of which each one must satisfy himself. It is not within the scope of this work to discuss the question.

APPENDIX A.

CHARACTERS AND REACTIONS OF THE PRINCIPAL ORGANIC SUBSTANCES FORMING THE HUMAN BODY.

Arranged alphabetically for purposes of reference.

ACIDS.

ACETIC ACID, $C_2H_4O_2$.—Transparent foliated crystals; change at 17° C. to a colourless fluid, of a piquant characteristic odour and of a very acid taste; volatile without residue. It is not precipitated by perchloride of iron, but if we dilute the acid by ammonia, the liquid becomes dark red (acetate of iron); white crystals are precipitated by the protonitrate of mercury.

BENZOIC ACID, $C_7H_6O_2$.—Silky needles; fusible at 120°; volatilizes at 150°; slightly soluble in cold water; soluble in alcohol and ether. (Its presence in normal urine is doubtful.)

BILIARY ACIDS.—They are two in number, glycocholic and taurocholic acids. See p. 38.

Pettenkofer's Test. — Add to the liquid a few drops of a solution of cane sugar and a few drops of concentrated sulphuric acid, when a rose and purple colour is produced. The presence of albuminoid substances keeps back the reaction.

Alkaline Salts of biliary acids, such as we find in the bile, dissolve cholesterine; they destroy the blood globules, and have the property of dissolving and emulsionizing fat.

BUTYRIC ACID, $C_4H_8O_2$.—Colourless liquid, of the odour of vinegar, or of rancid butter when it is impure, and soluble in water, alcohol, and ether; volatile at 160°; it is precipitated in concentrated solutions by chloride of calcium in oily drops. Heated with alcohol and sulphuric acid, it gives butyrate of ethyl, having an odour of strawberries.

Capric Acid, $C_{10}H_{20}O_2$.—Solid, of the odour of perspiration; fusible at 70°; slightly soluble in water; miscible in alcohol and ether in all proportions; the caprate of baryta is almost insoluble in cold water.

Caproic Acid, $C_6H_{12}O_2$.—Colourless liquid, oily, of the odour of perspiration; volatile at 202°; almost insoluble in water; miscible in alcohol and ether in all proportions; the caproate of baryta dissolves in twelve parts of cold water.

Caprylic, Acid $C_8H_{16}O_2$.—An oily liquid of the odour of perspiration; crystallizes at 12°; insoluble in water; miscible to alcohol and ether in all proportions; the caprylate of baryta is soluble in 125 parts of cold water.

Cholalic Acid, $C_{24}H_{40}O_5$.—Amorphous or crystallizes in quadrangular prisms from an etherial solution, or in octahedrons or tetrahedrons from an alcoholic solution; heated at 190° to 200°, it decomposes into dyslysine and water, thus: $C_{24}H_{40}O_5 = C_{24}H_{36}O_3 + 2H_2O$.

Damaluric Acid, $C_7H_{12}O_2$.—Oily liquid, denser than water; insoluble in this liquid.

Formic Acid, CH_2O_2.—Colourless liquid of a strong and piquant odour; volatile at 100° without residue; is not precipitated by the nitrate of mercury; heated with concentrated sulphuric acid, it decomposes into water and carbonic oxide $CH_2O_2 = CO + H_2O$.

Glycocholic Acid, $C_{26}H_{43}NO_6$.—Long slender needles; colourless; of a sweet taste; almost insoluble in cold water and in ether; soluble in hot water and alcohol, and in alkaline solutions; deviates polarized light to the right. Baryta water decomposes it into cholalic acid and glycocolle: $C_{26}H_{43}NO_6 + H_2O = C_{24}H_{40}O_5 + C_2H_5NO_2$. By boiling with sulphuric and nitric acids, it decomposes into choloidic acid and glycocolle: $C_{26}H_{43}NO_6$

$= C_{24}H_{38}O_4 + C_2H_5NO_2$. It forms with soda a salt which crystallizes in easily recognizable needles.

HIPPURIC ACID, $C_9H_9NO_3$.—Large crystals, white, hard and prismatic; inodorous, of a slightly bitter taste; soluble in water and hot alcohol, almost insoluble in ether; by the action of acids, it decomposes into benzoic acid and glycocolle: $C_9H_9NO_3 + H_2O = C_7H_6O_2 + C_2H_5NO_2$. Synthetically it may be obtained by combining chloride of benzole and glycocholate of zinc: $C_7H_5ClO + C_2H_4ZnNO_2 = C_9H_9NO_3 + ZnCl$.

Lücke's Test.—Evaporate the substance to be examined with an excess of nitric acid and heat the residue; an odour of bitter almonds may be perceived. This re-action also applies to benzoic acid.

INOSIC ACID, $C_{10}H_{14}N_4O_{11}$ (?).—A syrupy liquid, of the odour of soup, soluble in water; becomes a solid in alcohol. Its salts are crystallizable, soluble in water (except the metallic salts); insoluble in alcohol and ether.

LACTIC ACID, $C_3H_6O_3$.—A syrupy liquid, without colour or odour; of a very acid taste; soluble in water, alcohol, and ether.

MARGARIC ACID.—Mixture of palmitic acid and of stearic acid.

OLEIC ACID, $C_{18}H_{34}O_2$.—An oily liquid; yellow, inodorous, insipid; insoluble in water, soluble in alcohol, ether, and chloroform; exists as such at 14°; at 4° becomes a crystalline mass.

OXALIC ACID, $C_2H_2O_4$.—White crystals, of an acid taste; soluble in water; decomposed by sulphuric acid into carbonic acid and carbonic oxide: $C_2H_2O_4 = CO_2 + CO + H_2O$. Oxalate of lime crystallizes in four-cornered octahedrons.

PALMITIC ACID, $C_{16}H_{32}O_2$.—In crystalline masses, inodorous, insipid; fusible at 62°; insoluble in water, soluble in alcohol, very soluble in boiling alcohol, ether, and chloroform.

PHOSPHOGLYCERIC ACID, $C_3H_9PO_6$.—Syrupy liquid; easily decomposed by heat into glycerine and phosphoric acid. Its salts of baryta and of lime are soluble in cold water, insoluble in absolute alcohol.

PROPIONIC ACID, $C_3H_6O_2$.—Colourless liquid, of an odour similar to acetic acid; volatile at 142°; soluble in water; from an aqueous solution, chloride of calcium precipitates it in oily drops. Treated by alcohol and sulphuric acid, it gives out an odour of fruit, due to the formation of propionate of ethyl. The propionate of sodium is much more soluble than the acetate.

STEARIC ACID, $C_{18}H_{36}O_2$.—A crystalline mass, white, inodorous, insipid; fusible at 69°; insoluble in water, less soluble in alcohol than palmitic acid, soluble in boiling alcohol, ether, and chloroform.

TAUROCHOLIC ACID, $C_{26}H_{45}NSO_7$.—White amorphous powder, very bitter; soluble in water and alcohol, insoluble in ether; by baryta water and heat, it divides into cholalic acid and taurine: $C_{26}H_{45}NSO_7 + H_2O = C_{24}H_{40}O_5 + C_2H_7NSO_3$. By acids it decomposes into choloidic acid and taurine: $C_{26}H_{45}NSO_7 = C_{24}H_{38}O_4 + C_2H_7NSO_3$. The alkaline taurocholates are neutral; of a sweet taste, but bitter afterwards; soluble in water and in alcohol.

URIC ACID, $C_5H_4N_4O_3$.—Crystalline powder, colourless when pure, but generally yellow or brown. The microscope shows crystals, rhombohedric tables, or prisms having from four to six sides, or lozenge-shaped bodies. Insipid, inodorous; slightly soluble in water, insoluble in alcohol and ether.

Transformations of Uric Acid.—By bromine water, it is transformed into urea and alloxan: $C_5H_4N_4O_3 + Br_2 + 2H_2O = CH_4N_2O + C_4H_2N_2O_4 + 2HBr$. Alloxan yields by oxidation urea and carbonic acid: $C_4H_2N_2O_4 + 2O + H_2O = CH_4N_2O + 3CO_2$. Boiled with water and oxide of lead, uric acid yields allantoin and carbonic acid: $C_5H_4N_4O_3 + H_2O + O = C_4H_6N_4O_3 + CO_2$. In certain conditions of oxidation, it yields oxaluric acid: $C_3H_4N_2O_4$; ozone transforms it immediately into urea, carbonic acid, and ammonia. *Urates* are generally acid, and slightly soluble. Acetic and hydrochloric acids precipitate uric acid in the crystalline form. *Acid Urate of Soda* is found in urinary sediments as an amorphous powder, or in small spheres covered with prismatic needles. *Acid Urate of Ammonia* is an amorphous powder, dark and granulated. *Acid Urate of Lime* is a white amorphous powder, difficult to dissolve in water.

Reactions of Uric Acid.—(1) Put a little of the substance to be examined into a watch glass, add two drops of nitric acid, heat, and evaporate till dry; if the substance be uric acid, it dissolves in nitric acid, and gives by evaporation a yellow or reddish-yellow residue, which becomes reddish-purple by adding a drop of caustic ammonia, and bluish-violet with soda or potash. (2) Dissolve the substance to be examined in a drop of solution of caustic soda, and filter; add to the liquid chloride of ammonium in excess, and there will be a precipitate of urate of ammonia which, by the addition of hydrochloric acid, yields crystals of uric acid. (3) The microscopic examination of the crystals so as to determine their form.

Bases, &c.

Albumen of Serum.—When dried, it is a clear yellow, transparent, vitreous substance, soluble in water; the solution is somewhat opalescent, and lightly fluorescent. At 70°, heat coagulates it if the solution be not very alkaline. In this coagulation there always remains a small quantity of alkaline albuminate, and the liquid may even become alkaline. According to Mathieu and Urbain, the carbonic acid dissolved in the albumen combines with it under the influence of the heat, and is the cause of the coagulation. Solutions of albumen, deprived of carbonic acid by being placed in a vacuum, become incoagulable. Alcohol precipitates it from its solutions; carbonic, acetic, tartaric, phosphoric acids do not precipitate it; the concentrated acids precipitate it, especially nitric, metaphosphoric, picric, carbolic, and tannic acids. The alkalies transform it into basic albumen. It dissolves in concentrated nitric acid; most of the metallic salts precipitate it. After depriving it of all its salts by the dialyser, it is not precipitated by heat or alcohol, but is precipitated by ether. Deprived of its volatile salts, and especially of the carbonate of ammonia by the absolute vacuum, it is transformed into a matter said to be identical to fibrinogene and fibrinoplastic substances. Kept several days in the vacuum, at a temperature of 40° to 60°, it abandons considerable quantities of gas, consisting mostly of carbonic acid, hydrogen, and a small quantity of nitrogen. It deviates polarized light to the left.

ALBUMINOID MATTERS.—General characters of the albuminoid matters. They all contain nitrogen and sulphur; their chemical constitution oscillates around the following: $C_{54}H_7N_{16}O_{22}S$. Amorphous, soluble in water and various acids, usually soluble in alkalies; almost insoluble in alcohol and ether. Aqueous solutions are neutral. They yield in flame an odour of burned horn, separating ammoniacal products, and leaving a residue of ashes which consists mostly of phosphate of lime. Left to themselves, they decompose very easily. Calcined with potash or boiled with sulphuric acid, they furnish leucine and tyrosine. Concentrated nitric acid, when hot, transforms them into a yellow body, *xanthoproteic acid.* Treated by acids, alkalies, or by putrid decomposition, they yield the following products: oily volatile acids, oxalic, acetic, formic, valerianic, fumaric, and asparagic acids; leucine, tyrosine, ammonia, etc.; by oxidation of albumen, formic, acetic, propionic, butyric, valeric, capric, and benzoic acids, and the aldehydes of these acids, various organic volatile bases, acetonitrile, valeronitrile, and propionitrile may be obtained.

ALLANTOINE, $C_4H_6N_4O_3$.—Small transparent prismatic crystals, inodorous, insipid, neutral; soluble in cold water (160 parts), insoluble in cold alcohol and ether; soluble in boiling water and alcohol and in the alkaline carbonates.

BILIFUSCINE, $C_{16}H_{20}N_2O_4$.—A brown powder in mass, almost black, with a brilliant lustre; scarcely soluble in water, ether, and chloroform; soluble in alcohol with a brown colour, soluble in the alkalies with a reddish-brown colour. Its alkaline solution is precipitated brown by acids.

BILIRUBIN, $C_{16}H_{18}N_2O_3$. — An amorphous orange-coloured powder, or prismatic crystals, or in rhomboidal tables; insoluble in water; slightly soluble in ether, rather more in alcohol, very soluble in carbon disulphide, chloroform, and benzine. Its solutions are golden yellow. R. Maly has transformed it artificially into urobiline.

Gmelin's Test.—Pure nitric acid containing traces of nitrous acid, added with caution, produces a succession of tints in the following order: green, blue, violet, red, and yellow. The green tint must always be present to indicate bilirubin.

Biliverdin, $C_{16}H_{20}N_2O_5$ (?).—Dark-green amorphous powder, or green rhomboidal tables. Insoluble in water, ether, and chloroform; soluble in alcohol with a bluish-green colour, soluble in alkalies with a green tint; the acids precipitate green flakes from the solution. It gives Gmelin's test.

Casein.—Insoluble in water, soluble in waters lightly alkalinized. Its solution is not coagulated by heat. Soluble in hydrochloric acid, less in acetic acid. Its solutions are precipitated by alcohol, sulphate of magnesium, chloride of calcium, and metallic salts. By lengthened boiling with water, it gives lactic acid and creatinine.

Cholesterin, $C_{26}H_{44}O + H_2O$.—Crystallizes in slender, nacreous, rhombohedric tables, often irregularly indented at one angle. Neutral, insipid, inodorous. Insoluble in water; soluble in boiling alcohol; not saponifiable by potash. It gives a red colour with sulphuric acid, and blue or violet on adding iodine to concentrated sulphuric acid.

Chondrigene, $C_{49\cdot 9}\ H_{6\cdot 6}\ N_{14\cdot 5}\ S_{10\cdot 4}\ O_{28\cdot 6}$ %.—Fundamental substance of cartilages. Swells in water; by boiling in water, is transformed into chondrine.

Chondrine.—Same composition as chondrigene substance. Soluble in hot water; gelatinizes in the cold; insoluble in alcohol and ether. Its solutions are precipitated by alcohol as well as by mineral acids, acetic acid, alum, perchloride of iron, acetate of lead, and nitrate of silver; the precipitate is soluble in an excess of the reagent. The precipitate by acetic acid is redissolved by alkaline salts, which distinguishes chondrine from albuminoid matters.

Collagene.—Fundamental substance of bones and of connective tissue. It is softened by cold water, but does not swell. The ebullition transforms it into gelatine. It swells in weak acids. It is poorer in carbon and richer in nitrogen than albuminoid matters.

CREATINE, $C_4H_9N_3O_2$.—Rhombohedric prisms; colourless, sour; soluble in water, almost insoluble in alcohol, insoluble in ether; neutral. Heated with weak hydrochloric acid, it changes into creatinine: $C_4H_9N_3O_2 = C_4H_7N_3O + H_2O$. By ebullition with baryta, it transforms into urea and sarcosine: $C_4H_9N_3O_2 + H_2O = CH_4N_2O + C_3H_7NO_2$. By oxidation, it gives oxalic and carbonic acids and methyluramine: $C_2H_7N_3$.

CREATININE, $C_4H_7N_3O$.—Brilliant, colourless prisms of an alkaline taste; soluble in water and alcohol, scarcely soluble in ether; very alkaline. Oxidized, yields methyluramine: $C_2H_7N_3$. If we add to its solution a concentrated solution, not acid, of chloride of zinc, it produces a finely-granular precipitate, or in groups of needles or prisms (double chloride of zinc and of creatinine); this chloride, treated by sulphide of ammonium, reproduces creatine by taking an equivalent of water: $C_4H_7N_3O + H_2O = C_4H_9N_3O_2$.

CYSTINE, $C_3H_7NSO_2$.—Crystallizes in rhombohedric laminæ or colourless hexagons. Insoluble in water, alcohol, and ether; soluble in ammonia (distinctive character from uric acid), mineral acids, and oxalic acid.

ELASTINE, $C_{55\cdot5}\ H_{7\cdot4}\ N_{16\cdot7}\ O_{20}S$ % (?).—The base of elastic tissue. Yellow; insoluble in water, ammonia, acetic acid, and alcohol.

FIBRINE.—White amorphous filaments; insoluble in water, alcohol, and mineral acids; swells in weak acids and in solutions of alkaline salts; soluble in weak acids (acetic, lactic, and phosphoric acids), potash, solutions of alkaline salts, $\frac{1}{10}$ % solutions of chloride of sodium; ferrocyanide of potassium precipitates it from its acid, and acetic acids from its alkaline, solutions. Fibrine decomposes ozone, evolving oxygen without seeming to suffer change. With ozone and a few drops of tincture of guiacum, it gives a blue colour.

FIBRINOGENE.—Soluble in water; carbonic acid gives a precipitate which forms with difficulty; precipitated by a mixture of

3 parts of alcohol to 1 part of ether; precipitated by sulphate of copper; the precipitate is insoluble in an excess of the reagent.

FIBRINOPLASTINE.—Soluble in aërated water; precipitated in flakes by carbonic acid, not by alcohol. It is precipitated by mineral acids; the precipitate is insoluble in an excess of the reagent; it is also precipitated by mineral salts, when it is insoluble in an excess of the reagent. If we add fibrinoplastic substance to a salt solution of fibrinogene, it produces fibrine.

GELATINE.—Whitish-yellow; swells in cold water; soluble in boiling water, and gelatinizes on cooling; soluble in acids and alkalies. Solutions of gelatine are precipitated by tannin and bichloride of mercury; they are not precipitated by mineral acids, bases, acetic acid, and ferrocyanide of potassium; deviates ray of polarized light to the left.

GLOBULINE.—Albuminoid matter; insoluble in water, soluble in a strong solution of chloride of sodium; its solution coagulated by heat; changed into syntonine by strong hydrochloric acid. According to Hoppe-Seyler, it includes vitelline, myosine, fibrinogene, and fibrinoplastic substances.

GLYCOGENE, $C_6H_{10}O_5$. — Amorphous, colourless, inodorous; soluble in water with opalescence, insoluble in alcohol and ether.

GLUCOSE, $C_6H_{12}O_6$.—Amorphous or crystallized; colourless; sweet; slightly soluble in water, soluble in alcohol, insoluble in ether. With yeast, it undergoes alcoholic fermentation, and produces alcohol and carbonic acid: $C_6H_{12}O_6 = 2C_2H_6O + 2CO_2$.

Principal Tests (the liquid to be examined must be wholly free from albuminoid substances):—

1. *Fehling's Test.*—To prepare Fehling's solution, dissolve 34·65 grammes of sulphate of copper in 160 grammes of water; then dissolve 173 grammes of double tartrate of potash and soda in 650 cubic centimetres of a solution of soda having a density of 1·12; pour the mixture into a glass gauged to a litre, and add water sufficient to make a litre. Glucose acts on the fluid while hot, and gives a red precipitate of oxide of copper; the precipitate is only produced in an alkaline fluid; the presence of colouring matters impedes the reaction, and sometimes necessitates the

previous discoloration by animal charcoal. It must not be heated beyond 70°.

2. *Moore's Test.*—Add to the liquid a solution of caustic potash, or of caustic soda, until the reaction be strongly alkaline, and boil; if it contain glucose, it will become yellow, then reddish-brown, and next dark-brown or black.

3. Fermentation with yeast.

4. Microscopic examination of the crystals of glucose, and of the combination of glucose and chloride of sodium (rhombohedric plates and crystalline pyramids having 4 and 6 facets).

5. Examine with saccharimetre, which shows the presence of sugar by the effect on polarized light.

HÆMATINE, $C_{34}H_{34}N_4FeO_5$ (*Hoppe-Seyler*).—Reddish-brown powder; metallic-like, not crystallizable; insoluble in water, alcohol, and chloroform; soluble in acidulated alcohol and alkalies. By the action of dilute sulphuric acid, it gives two bodies containing iron, namely, hæmatoporphyrine and hæmatoline (*Hoppe-Seyler*). It forms with hydrochloric acid a combination, *hemine of Teichmann*, which crystallizes in rhombohedral dark-brown plates; insoluble in water, scarcely soluble in hot water and ether, but soluble in potash. In order to see these crystals, it is sufficient to evaporate on a glass plate a few drops of water reddened by blood; add to the residue glacial acetic acid, and evaporate near a fire, having covered all with a glass plate.

HÆMATOIDINE.—Hard, red crystals produced in blood-clots (bilirubin).

HÆMOGLOBINE: empirical formula, $C_{600}H_{960}N_{154}FeS_3O_{179}$ (*Preyer*).—Red, microscopic crystals, lozenges, and four-sided prisms; soluble in water, giving it a blood-red colour; heat and the presence of alkalies augment its solubility; its solutions are muddy between 70° and 80°; it is decomposed by all agents which modify albuminoid substances; its products of decomposition are—hematine, an albuminoidal coagulable matter, formic and butyric acids, and other volatile fatty acids.

Hæmoglobine forms with oxygen a combination: oxyhæmoglobine; 1 gramme of dried hæmoglobine absorbs on an average 1 cubic centimetre of oxygen; this oxygen can be dispelled by the vacuum, heat, or reducing agents (reduced hæmoglobine); oxy-hæmoglobine crystallizes more easily than reduced hæmoglobine, p. 295.

HYPOXANTHINE, $C_5H_4N_4O$.—Microscopic crystals composed of very fine colourless needles; slightly soluble in water, insoluble in alcohol and ether.

INDICAN, $C_{26}H_{31}NO_{17}$.—Light brown syrupy liquid; bitter and nauseous in taste; soluble in water, alcohol, and ether; with alkaline liquids, it gives the test of glucose. Heat decomposes it into indicanine and indiglucine: $C_{26}H_{31}NO_{17} + H_2O = C_{20}H_{23}NO_{12} + C_6H_{10}O_6$. By concentrated hydrochloric acid, it decomposes into indigo and indiglucine: $C_{26}H_{31}NO_{17} + 2H_2O = C_8H_5NO + 3C_6H_{10}O_6$. Indigo in its turn yields, on hydration, leucine and formic acid: $C_8H_5NO + 5H_2O = C_6H_{13}NO_2 + CH_2O_2 + CO_2$. Indiglucine has a sweet taste, and reduces oxide of copper, but does not cause the alcoholic fermentation.

INOSITE, $C_6H_{12}O_6 + 2H_2O$.—Large colourless crystals; soluble in water, but insoluble in alcohol and ether; of a sweet taste; dissolves hydrated oxide of copper without reducing it by heat.

LEUCINE, $C_6H_{13}NO_2$.—Fine, brilliantly-white crystals, often united in spheres or round refracting masses. Insipid; inodorous; soluble in water, and almost in alcohol, but not in ether; neutral. By oxidation by alkaline permanganate of potash, it is split up into oxalic, valeric, and carbonic acids, and ammonia.

MUCINE, $C_{48}.\ H_6.\ N_8.\ O_{35}$.—Swells in water, without dissolving; its solution precipitates by alcohol, by weak acids, and acetic acid; it is not coagulated by heat. Alkaline or neutral solutions of mucine are not precipitated by sulphate of copper, bichloride of mercury, nitrate of silver, perchloride of iron, &c.

MYOSINE.—Soluble in alkaline solutions, especially in chloride of sodium; transformed by weak acids into syntonine; its saline solution is coagulated by heat like albumen; alcohol precipitates it.

OLEINE, $C_{57}H_{104}O_6$ or $C_3H_5\ (C_{18}H_{33}O)_3O_3$.—Liquid at ordinary temperatures, colourless; easily oxidized by air, becoming yellow; soluble in absolute alcohol; dissolves palmitine and stearine. Represents the principal mass of fatty bodies.

Palmitine, $C_{51}H_{98}O_6$ or $C_3H_5\ (C_{16}H_{31}O)_3O_3$.—Crystallizes in fine needles, often radiated round a centre; soluble in boiling alcohol and ether. Melting point very variable from 46° to 63°.

Paralbumine.—Distinguished from the albumen of serum by two characters: the precipitate obtained by alcohol is soluble in water; it coagulates incompletely by heat.

Peptones.—Distinguished from other albuminoid substances by the following characters: they are soluble in water, insoluble in absolute alcohol and ether, but alcohol precipitates them with difficulty from an aqueous solution; heat does not coagulate them; they are neither precipitated by acids nor by alkalies, but they are precipitated by bichloride of mercury, or acetate of lead, or ammonia; ferrocyanide of potassium, and acetic acid throw down a precipitate. They are very diffusible. They deviate to the left the plane of a ray of polarized light.

Plasmine of Denis.—Soft, white, amorphous mass, precipitated from blood plasma by the addition of common salt; divides in coagulation into fibrin or ordinary fibrin and soluble fibrin, which remains dissolved in the salt-plasma.

Protagon.—A neutral substance, insoluble in water and ether, soluble in boiling alcohol and in fats. Heated with baryta water, it yields, among other products, glucose, phosphoglyceric acid, and a body almost identical with neurine, but which differs by H_2O less, and has for a formula $C_5H_{13}NO$; this body reproduces neurine by the simple action of water on its salts. According to Hoppe-Seyler, protagon is a mixture of lecithine and cerebrine; Baeyer considers it a glucoside.

Sarcosine, $C_3H_7NO_2$.—The superior homologe of glycocolle or methylglycocolle. Formed in treating creatine while hot with baryta water. Crystallizes in rhombohedric colourless crystals; very soluble in water, slightly in alcohol, but not in ether.

Stearine, $C_{57}H_{110}O_6$ or $C_3H_5\ (C_{18}H_{35}O)_3O_3$. Less soluble than other fats in boiling alcohol and ether; crystallizes in rectangular tablets. More rarely in rhombohedric prisms. Melting point about 60°

Syntonine.—It is distinguished from basic albumen, because its solution in weak acids and alkaline carbonates is precipitated by neutralization (even in presence of alkaline phosphates). It has two other principal tests: (1) its solution in lime water is partly coagulated by heat; (2) the same solution gives a precipitate, while hot, with chloride of calcium, sulphate of magnesia, and chloride of sodium.

TYROSINE, $C_9H_{11}NO_3$. — Crystallizes in slender, colourless, microscopic needles; insipid, inodorous; slightly soluble in cold water, but insoluble in alcohol and ether. While burning, it smells like burnt horn. When oxidized by bichromate of potash and sulphuric acid, it yields oil of bitter almonds, and hydrocyanic, benzoic, formic, acetic, and carbonic acids.

UREA, CH_4N_2O.—Elongated, prismatic, four-sided crystals terminated by one or two oblique surfaces. Inodorous; of a fresh, bitter taste; soluble in water and alcohol, but not in ether. It is neither precipitated by acetate nor by subacetate of lead, but by mercuric nitrate.

Millon's Test.—Chlorine water, hypochlorite and hypobromite of sodium decompose it into nitrogen and carbonic acid. It is easily decomposed into carbonic acid and ammonia (heat, fermentation of urine, acids, &c.); in fact it represents carbonate of ammonium less two molecules of water.

Nitric acid precipitates the urea in octahedric crystals, in lozenge-shaped tablets, and hexagons of nitrate of urea; oxalic acid gives flat or prismatic crystals of oxalate of urea.

UROBILINE, $C_{32}H_{40}N_4O_7$.—Yellow amorphous mass; soluble in water and ether, slightly soluble in alcohol. Fluorescent; produces absorption bands in the spectrum between *b* and F. It does not respond to Gmelin's test.

UROGLAUCINE, C_8H_5NO.—Identical with indigo. Derived from indican. Blue powder, formed of microscopic needles; insoluble in water and sulphuric acid, slightly soluble in alcohol.

XANTHINE, $C_5H_4N_4O_2$.—Pale-yellow amorphous powder or crystallized plates; scarcely soluble in water, insoluble in alcohol and ether, soluble in caustic ammonia.

APPENDIX B.

ANIMAL ELECTRICITY.

1. A Short Account of the Discovery of Animal Electricity.[1]

The discovery of animal electricity dates from 1786. It is said that Madame Galvani, on preparing some frogs for culinary purposes, observed that the apparently dead animals became convulsed when brought into the neighbourhood of an electrical machine in action. Her husband, who was professor of anatomy and physiology in Bologna, had his attention directed to these phenomena, and found that the convulsions occurred at the instant a spark was emitted from the conductor, provided some metallic substance was in contact with the nerve of the frog. He tried the same experiment with lightning, and, in the autumn of the same year, endeavoured to discover the action of atmospheric electricity on the prepared legs of a frog when the sky was stormless. On the 20th of September, he suspended three frogs to the iron trellis-work surrounding the roof of his house, by means of copper hooks, and saw, when they were blown about by the wind, that convulsions were caused whenever they came in contact with the iron. This observation convinced him that an electrical machine was not required, the same effect being produced on the contact of dissimilar metals. He at length concluded that the convulsions were due to inherent electricity, that is, electricity secreted in and originating from the animal tissues.

---

[1] Prepared by the author for Hughes Bennett's Text-book of Physiology in 1871.

Galvani published an account of his experiments in 1791. At this time the existence of a "nervous fluid," a something which, if not life itself, was considered inseparable from it, was keenly debated by the learned, and contended for by the animists. Galvani's discovery, therefore, riveted the attention of the scientific world—electricity took the place of the nervous fluid, and the entire source of life, as well as the origin of the bodily and mental functions, were now ascribed to the existence of a new principle, which, from the name of its discoverer, was called *Galvanism.*

Among the many distinguished men whose attention was attracted towards Galvani's discovery, the most remarkable was Alexander Volta. He was a physicist and professor of natural philosophy in the University of Pavia. At first he entered fully into the views of his countryman, and repeated his experiments. But in his hands galvanism, instead of taking a physiological and medical, took a physical, direction. Finding that muscular contractions in a frog could be produced only by the contact of dissimilar metals, he at length dissented from Galvani's theory of animal electricity. Trying by the same means to produce muscular contractions in the human body, he failed. But on placing a metal above and below the tongue, he detected a peculiar taste at the moment of contact. This experiment had been previously recorded by Sulzer, and laid aside only as curious, but in the hands of Volta it became the groundwork of chemical, or what has been called *Voltaic*, electricity. In opposition to Galvani, therefore, he put forth the opinion that the muscular contractions in the frog had nothing to do with animal, but were caused by a very feeble *artificial*, electricity, which was produced by the application of heterogeneous metals to the limbs of the animals.

In reply to this attack, Galvani pointed out that the contractions might be occasioned by one metal; but Volta then showed that the two extremities or surfaces of one piece of metal might be in different states of tension, and therefore capable of exciting electricity. Galvani then used mercury alone, to which this objection could not apply, and dipping the muscles into one part of a trough filled with it, he thus succeeded in causing contractions. But Volta, by a new series of experiments, demonstrated that mercury was always altering under the action of the air, and that, in conjunction with moisture, it could produce electricity independent of an animal. It now became necessary for Galvani to show that contractions took place without any metal at all, and, aided by his nephew Aldini, he succeeded in doing so, and, as he thought, in for ever silencing his formidable opponent. In fact, he discovered that on dissecting out the crural nerve, but leaving one end in connection with the leg, and bringing this nerve in contact with the muscles externally, the latter were thrown into distinct contractions. He also caused the limb to contract by simply bringing the nerve in contact with the muscle of another animal insulated from the limb.

His theory of animal electricity now was, that it was produced in the nervous system, and especially in the cerebrum. The internal substance of nerves he considered to have great conducting powers, but their oily surfaces prevented dispersion through the body, and allowed its accumulation in the muscles. These last he compared to a Leyden jar, the outer surface being negative, the internal positive. The nerve was analogous to the conductor of the jar. When the nerve connects the inner with the outer surface, there is a discharge of electricity, causing irritation and contraction of the muscles.

Volta at first endeavoured to meet these facts by the supposition of a mechanical stimulation of the nerves, but at length showed that, if not caused by metals, it was necessary that there should be dissimilar fluids and tissues which were capable of exciting electricity. It was admitted, even by Galvani's followers, that it was essential to the success of the experiment that the muscle with which the nerve was in contact should be moistened with blood or some thick fluid, and if by any accident the limb remained motionless, it was only necessary, in order to induce muscular contractions, that the parts to be in contact should be moistened with saliva, brine, mucus, &c., or still better, with soapy water, and best of all, with an acid or alkaline solution.

Galvani, in several letters to Spallanzani, endeavoured to weaken the force of these arguments, as did Humboldt, who showed that contractions resulted when the circuit consisted only of nerve and muscle, without the interposition of blood, mucus, &c. About this time, 1798, Galvani fell ill, and died on the 4th December of that year. Volta's experiments, on the other hand, were continued with unabated energy, and, towards the end of 1799, he discovered the Voltaic battery, whereby his opinions and the production of electricity by the contact of metals and a fluid was completely proved. This great victory, which Galvani, by his death, escaped the mortification of experiencing, notwithstanding the support of Humboldt, Aldini, Pfaff, and a few others, overthrew the idea of an animal electricity for the space of twenty-eight years. During this period, indeed, its existence was generally regarded with incredulity; and the term *animal magnetism*, adopted by impostors, only tended to bring it still more into contempt. Volta died in 1826, and it is curious that only a year afterwards, Nobili again revived animal electricity, by demonstrating the existence of an electrical current in the frog. In the interval of twenty-eight years, Voltaic electricity made the most wonderful progress. In the hands of Sir Humphrey Davy, it led to the most brilliant discoveries in chemistry, and its subsequent applications to the production of motor power in various ways, and to communication between distant parts of the earth, constitute some of the wonders of physical science in the present age.

In 1820, Oersted, a Danish philosopher, discovered electromagnetism. He showed that when a continuous galvanic current passes along a wire, placed above or below, and parallel to, a magnetic needle, the latter is immediately deflected. This led Ampère to construct the astatic needle, and in turn enabled Nobili to construct a galvanometer, which he rendered exquisitely sensitive by various improvements. He prepared a frog after the method of Galvani, and, having introduced its two legs into two glasses of salt water, he reunited the two vessels by filaments of moist cotton; the frog's muscles at once contracted. Removing the cotton, he connected the two glasses by means of the galvanometer circuit, and he observed a deviation of from 10° to 30°, showing that *an electrical current was passing from the feet to the head of the animal.* By introducing several frogs into the circuit, he increased the strength of the current.

The galvanometer of Nobili enabled physiologists to demonstrate that Galvani and Volta were both right and both wrong. Galvani was right in maintaining the existence of an inherent animal electricity, whilst he was wrong in supposing that the contact of two metals with the tissues was a proof of this. Volta, again, was right in maintaining that galvanism could be produced independently of animals, but wrong in denying that electrical currents existed in them. By the astatic needle, as Du Bois-Reymond happily remarks, metallic electricity was enabled to atone for the wrong she had done to her more tender twin sister in their earlier years.

Whilst Nobili, by his construction of a galvanometer, was of such essential service, he was led into an error, viz., that the deflection of the needle was due to thermo-electricity. It was ten years later, in 1837, that Professor Matteucci, of Pisa, showed that to obtain a deviation of the galvanometer needle, it was not necessary to prepare the frog according to Galvani's method. On connecting any two parts of its body, as, for example, the head and legs, by means of the galvanometer, he at once obtained a deviation. In 1841, he advanced the following law: "The interior of a muscle, placed in connection with any part whatever of the same animal, such as nerve, surface of muscle, skin, &c., produces a current which goes in the animal from the muscular part to that which is not so." In this paper, he first described his muscular *pile*, consisting of about twenty frogs' thighs roughly cut across, and arranged end to end. By connecting the stump of the knee with one wire leading to the galvanometer, and the section of the femur with the other, the needle was at once deflected so as to indicate a current passing upwards in the pile from the knee to the thigh. He considered this to be a current different from the frog current of Nobili, and he held that the frog had two currents (1) the muscular current (Nobili's) common to all animals; and (2) the special current, evolved by the muscular pile, peculiar to the frog.

In 1841, Professor Emil Du Bois-Reymond, of Berlin, repeated Matteucci's experiments, and further investigated the subject with the aid of the most delicate galvanometers, and other ingenious apparatus constructed by himself. From this period a new impulse was given to experimental physiology by the aid of modern instruments of precision.

2. General Phenomena of Electrical Fishes.[1]

Certain fishes have special organs for the development of electricity, by means of which they have the power of communicating a shock to other animals, a power they use either for self-defence or for paralyzing their prey. The most remarkable of these fishes are :—

1. The *Torpedo.*—This fish, a species of ray termed by naturalists *Torpedo Galvani*, after the celebrated Bologna Professor, is a native of the Mediterranean. It is sometimes found in the Atlantic, rarely in the North Sea. Its powers of giving benumbing shocks was recognized by fishermen before the days of Aristotle, who carefully describes them. J. Walsh was the first, in 1773, to show experimentally that these shocks of the torpedo were essentially electrical. The electric organs, two in number, are large, flat, kidney-shaped bodies, placed on each side of the head and gills. The organ is composed of a mass of hexagonal prisms, placed vertically between the dorsal and abdominal integuments, and each prism is divided by a series of delicate membraneous plates or diaphragms attached by their angles to the aponeurotic sheaths separating the prisms. The plates are separated from each other by a jelly-like albuminous fluid. In each organ there are from 400 to 1000 prisms, and it has been estimated that there are about 2000 plates in each prism. This powerful electric battery, thus divided into compartments, is richly supplied with large nerves. These are (1) a large branch from the trigeminal, and (2) four branches from the vagus which spring from a large trunk on each side of the forepart of the medulla oblongata. According to Paccini, the nerves enter the laminæ at the points of their attachment to the prisms, and are distributed to their under surface, and in the fluid between that surface and the next laminæ. They ramify here in a very vascular nucleated tissue. The upper or dorsal surface of the dia-

---

[1] The information here given has been derived chiefly from two papers, written by the late Professor John Goodsir (*Anatomical Memoirs*).

phragm is negative, while the under surface, on which the nerves are distributed, is positive. Each prism is thus analogous to a voltaic pile. In the torpedo the piles are vertical, and the plates horizontal.

2. The *Gymnotus electricus* is an eel-like fish, common in the lakes and rivers of South America, especially in Guiana. It possesses four electric organs, two on each side, stretching from the pectoral fins to near the end of the tail. The proportional size of the electric organs to the body is much greater in the gymnotus than in the torpedo, the viscera of the animal occupying only a small portion of the anterior part of the body. Each electric organ consists of a series of horizontal membranes or plates arranged in the longitudinal axis of the body nearly parallel to each other. The organ thus resembles a series of galvanic troughs. Each trough is divided by their vertical laminæ or diaphragms. Each lamina is not simple as in the torpedo, but according to Paccini, it consists of two layers separated by a fluid. The posterior layer is a delicate fibrous structure, and in it alone the nerves ramify. It is the positive element of the battery. The anterior is composed of vascular nucleated tissue, and it is the negative element. The fluid between the two layers of the laminæ differs in character from that in the interspace between the posterior and the anterior layer of the next lamina, but both fluids are of an albuminous character. The electric battery of a gymnotus, therefore, does not resemble a voltaic pile with one liquid, but a voltaic battery with two fluids. In the gymnotus, the batteries are horizontal and the plates vertical, the opposite arrangement to that described in the torpedo. The electric organs are richly supplied by the abdominal branches of the spinal nerves, and it is remarkable that they receive no branches from the trigeminal and vagus, which supply those from the torpedo.

3. The *Malapterurus electricus*, Rassch, or thunder-fish of the Arabs, is a native of the Nile, Niger, and other African rivers. The electric organ forms a layer beneath the skin enveloping the whole body, with the exception of the head and fins. An insulating layer of fat separates it from the subjacent muscles. The laminæ are traversed by numerous very delicate decussating

membranes, which are divided into lozenge-shaped cells filled with an albuminous fluid, a large nerve trunk from the commencement of the cord supplies the organ. This is distributed to the abdominal or posterior surface of the electrical laminæ, forms a conoidal expansion, and then pierces the centre of the plate, distributing its branches to the anterior or thoracic surface, which is the positive one.

4. In addition to these, the *Mormyrus longipinnis*, a fish allied to the pike family, found in the Nile ; the *Rhinobatus electricus*, a ray from Brazilian waters ; the *Tetraodon electricus*, an eel also found in the Nile ; and the *Trichiurus electricus*, a ribbon-like fish found in the Indian Ocean, are said to possess electrical properties, but not to the extent manifested by the three fishes we have more particularly described. In the common skate, *Raia batis*, there is an organ, first described by Dr. Stark in 1844, and afterwards by Robin, which structurally resembles a voltaic pile ; but its electro-motor power has never been tested.

General Properties of Electric Fishes.—The electricity generated by these fishes has considerable tension, and is capable of developing the electric spark, of magnetizing steel, of decomposing iodide of potassium, and of affecting a galvanometer. In order to receive a shock, an animal must be in communication with the electric fish at two points, so as to complete the circuit, but the circuit may be completed by the earth. According to Matteucci and Savi, an insulated frog's leg does not contract when the extremity of the nerve attached to it is brought in contact with a torpedo, but the instant a second point of contact is made, powerful contraction ensues. Matteucci also found that while the electric organ was in operation no current traversed the nerves. According to Bilharz, the nerves are always distributed to the positive side of the electric plate, a law which anatomical researches has fully confirmed. Thus, in the *torpedo*, the electric current passes from the belly to the back ; in the *gymnotus* it passes from the tail to the head, and the most powerful shock is experienced on grasping the head with the right hand and the tail with the left. As the hands are approximated the shock becomes weaker. In the *malapterurus* the current flows from the head to the tail The gymnotus transmits a more powerful shock than the torpedo, and Humboldt states that so powerful an animal as the horse may be killed by a full-grown gymnotus.

The phenomena manifested by electric fishes are of great interest, because they afford an instance of the relation existing between vital and physical forces. That the organs can develope electricity to a considerable amount only when provided with a proper nervous supply, is proved by the fact that when the nerves are divided no shock is transmitted, but on irritating the distal end of the nerve, the electric discharge is at once felt. Matteucci, however, states that when a fragment of the electric organ of a torpedo was brought into connection with a galvanometer, the needle was deflected to an angle of from 20° to 30°, indicating that for a time the electric organ retains a portion of its activity even after all nervous and vascular connection had been severed. The nerve influence, transmitted from the nervous centres of the animal, probably excites, in some way or other, nutritive changes in particular portions of the battery, electrical disturbance is thus occasioned, and a current passes through the structure. This is produced, according to Du Bois-Reymond, by the same polar action as exists in muscles. As the battery in all electrical fishes is imperfectly insulated, being surrounded by water—a good conducting medium—a large quantity of electricity is lost by diffusion, but so much electricity is evolved that the animal can afford to lose a proportion of it. When, as a result of irritation, a torpedo sends a shock into the body of an animal, the mechanism of the act is that of a reflex or diastolic action ; and, it is confirmatory of this view, that such a poison as strychnia, which excites the reflex motor centres, causes the electric organs to emit a quick succession of involuntary electric discharges, a fact observed by Matteucci and Savi. But the action is also under the control of the will of the animal. In transmitting several powerful shocks the electric organ is rapidly exhausted, and the animal requires an interval of repose and nourishment to recover the loss of nervous energy it has sustained.

APPENDIX C.

REFERENCE TABLES OF SIZE, WEIGHTS, AND SPECIFIC GRAVITY,

Arranged by John Barlow, M.B., *Muirhead Demonstrator in Physiology in the University of Glasgow.*

I.—Size and Weight of different parts of Body.

1. The Nervous System.

		Length.	Breadth.	Thickness.	Weight.	
Brain,	Medulla .	1¼ in.	1 in.	¾ in.	1 oz.	
	Cerebellum, .	3½-4 in.	2½ in.	2 in.	5 oz.	
	Cerebrum, .	—	—	—	44 oz.	
						50 oz.
Spinal Cord, . .		17 in.	¾ in.	¾ in.		1½ oz.

2. The Digestive System.

a. *The Canal.*

	Length.	Breadth.	Weight.
Pharynx, . . .	4½ in.	—	—
Œsophagus, . .	9 in.	—	—
Stomach, . . .	10-12 in.	4-5 in.	5 oz.
Duodenum, . . .	12 in.	1½-2 in.	—
Jejunum, . . .	8 ft.	—	—
Ileum, . . .	12 ft.	—	—
Cæcum, . . .	2½ in.	2½ in.	—
Appendix vermif., .	3-6 in.	—	—
Colon, ...	5 ft.	—	—
Rectum, . . .	7 in.	—	—

b. *Glands connected with the Canal.*

	Length.	Breadth.	Thickness.	Weight.
Parotid, . . .	—	—	—	5-8 drs.
Sublingual, . .	—	—	—	2½ drs.
Submaxillary, .	—	—	—	1 dr.
Tonsils, . . .	½ in.	⅓ in.	⅓ in.	1 dr.
Liver, . . .	10-12 in.	6-7 in.	3½ in.	50-60 oz.
Pancreas, . .	6-8 in.	1½ in.	½-1 in.	2·3 oz.

3. The Vascular System.

		Length.	Breadth.	Thickness.	Weight.
Blood Glands,	Spleen, . . .	5 in.	3-4 in.	1-1½ in.	5-7 oz.
	Suprarenal capsules,	1½ in.	1¼ in.	⅙ in.	2 drs.
	Thymus gland, .	2 in.	1¼ in.	¾ in.	1-2 oz.
	Thyroid ,, .	2 in.	1¼ in.	¾ in.	1-2 oz.
Heart, ...		5 in.	3½ in.	2½ in.	11 oz. M.;[1] 9 F.[1]

Circumference of Orifices of Heart,	Auriculo ventricular,	Right, .	4-6 in. M.; 4 F.
		Left, .	3-10 in. M.; 3-7 F.
	Arterial, . . .	Right, .	3-4 in. M.; 3-3 F.
		Left, .	3 in. M.; 2-10 F.

4. Respiratory System.

		Length.	Breadth.	Weight.
Trachea, . . .		4½ in.	¾-1 in.	—
Bronchus,	Right, .	1 in.	½ in.	—
	Left, .	2 in.	⅜ in.	—
Vocal Cords, . .		7 lines M.; 5 F.	—	—
Lungs,	Right, .	—	—	24 oz. M.; 17 F.
	Left, .	—	—	21 oz. M.; 15 F.

5. Urinary and Reproductive Systems.

	Length.	Breadth.	Thickness.	Weight.
Kidney, ...	4 in.	2½ in.	1¼ in.	4½ oz.
Bladder (*moderately distended*),	5 in.	3 in.	—	—
Prostate gland, . .	1½ in.	1¼ in.	1 in.	6 drs.
Testes, ...	1½ in.	1¼ in.	1 in.	6 drs.
Uterus, ...	3 in.	2 in.	1 in.	7-12 drs.
Ovary, ...	1½ in.	¾ in.	½ in.	1-2 drs.
Vagina, ...	4-6 in.	—	—	—
Penis, ...	7 in.	—	—	—

---

[1] M., male; F., female.

II. —Size of different Histological Elements (Glands, Cells, Tubes, and Fibres) in *fractions of an inch.* They are arranged alphabetically.

1. *Glands.*

Gastric,	$\frac{1}{60}$ - $\frac{1}{20}$	in. long;	$\frac{1}{400}$ in. diameter.
Lieberkühn,	$\frac{1}{360}$ - $\frac{1}{60}$	,,	$\frac{1}{600}$,,
Malpighian Body, in spleen,	$\frac{1}{70}$	,,	—
Malpighian Body, in kidney,	$\frac{1}{120}$	,,	—
Peyer's patches,	$\frac{1}{2}$-4	,,	$\frac{1}{2}$ in. broad.

2. *Cells.*

	Breadth.	Thickness.
Air cells,	$\frac{1}{150}$ - $\frac{1}{70}$ in.	—
Blood corpuscles, coloured, of man,	$\frac{1}{3200}$ in.	$\frac{1}{12400}$ in.
,, ,, fœtus,	$\frac{1}{2800}$ in.	—
,, ,, elephant,	$\frac{1}{2750}$ in.	—
,, ,, musk-deer,	$\frac{1}{6300}$ in.	—
,, ,, camel,	$\frac{1}{3250}$ - $\frac{1}{500}$ in.	—
,, ,, pigeon,	$\frac{1}{2314}$ - $\frac{1}{3400}$ in.	—
,, ,, frog,	$\frac{1}{1230}$ - $\frac{1}{2286}$ in.	—
,, ,, proteus,	$\frac{1}{400}$ - $\frac{1}{720}$ in.	—
,, ,, pike,	$\frac{1}{2000}$ - $\frac{1}{3500}$ in.	—
,, ,, shark,	$\frac{1}{1143}$ - $\frac{1}{1684}$ in.	—
,, ,, earthworm,	$\frac{1}{110}$ - $\frac{1}{1200}$ in.	—
,, ,, leech,	$\frac{1}{3000}$ in.	—
Blood corpuscles, colourless, of man,	$\frac{1}{2400}$ - $\frac{1}{1000}$ in.	—
Cartilage cells,	$\frac{1}{900}$ - $\frac{1}{1400}$ in.	—
Cilia,	$\frac{1}{4000}$ - $\frac{1}{2500}$ in.	—
Chyle corpuscles,	$\frac{1}{2500}$ in.	—
Chyle molecules,	$\frac{1}{30000}$ in.	—
Epithelial cells,	$\frac{1}{1500}$ - $\frac{1}{3500}$ in.	—
,, ,, nuclei of,	$\frac{1}{4000}$ - $\frac{1}{6000}$ in.	—
Fat cells,	$\frac{1}{300}$ - $\frac{1}{600}$ in.	—
Lacuna of bone,	$\frac{1}{1200}$ in. long;	$\frac{1}{2500}$ broad.
Pus cells,	$\frac{1}{2000}$ in. broad.	—
Ovum,	$\frac{1}{100}$ in. ,,	—
,, germinal vesicle of,	$\frac{1}{720}$ in. ,,	—
,, germinal spot of,	$\frac{1}{3000}$ in. ,,	—
Spermatozoa,	$\frac{1}{500}$ in. long.	—
,, body of,	$\frac{1}{10000}$ in. diameter.	—

3. *Tubes.*

Bloodvessels, Fine,	$\frac{1}{1200}$ - $\frac{1}{100}$	in. diameter.
Bloodvessels, Medium,	$\frac{1}{60}$ - $\frac{1}{100}$	,,
Capillaries,	$\frac{1}{1500}$ - $\frac{1}{3000}$	,,
Canals, Haversian,	$\frac{1}{1000}$ - $\frac{1}{200}$	,,
Canaliculus in bone,	$\frac{1}{7000}$	,,
Dentine,	$\frac{1}{5000}$ - $\frac{1}{10000}$	,,
Urinary tubules,	$\frac{1}{240}$ - $\frac{1}{600}$	,,

4. *Fibres.*

Enamel,	$\frac{1}{5000}$	in. diameter.
Muscle, striated,	$\frac{1}{400}$	,,
,, striæ of,	$\frac{1}{17000}$	,,
Nerve fibres, white,	$\frac{1}{12000}$ - $\frac{1}{5000}$	,,
,, grey,	$\frac{1}{6000}$ - $\frac{1}{3000}$	,,
White fibrous tissue,	$\frac{1}{25000}$	,,
Yellow elastic,	$\frac{1}{24000}$ - $\frac{1}{4000}$	,,

III.—MEASURES of LENGTH of various DUCTS and CANALS in the Human Body.

	In.		In.
Bile duct,	3	Testicle (*vas deferens*),	20
Cowper's gland, duct of,	$1\frac{1}{4}$	Eustachian tube,	$1\frac{3}{4}$
Ejaculatory duct,	$1\frac{1}{4}$	Meatus auditorius externus,	$1\frac{1}{4}$
Hepatic ,,	2	Urethra, Male,	8
Nasal ,,	$\frac{3}{4}$	Urethra, Female,	$1\frac{1}{2}$
Parotid ,,	$2\frac{1}{2}$	Ureter,	16
Submaxillary ,,	2		

IV.—SIZE of the more important parts in connection with ORGANS OF SPECIAL SENSE.

COCHLEA (*Waldeyer*).

Lamina spiralis membranacea: total length in man,	30	mm.
Reissnerian membrane, length of, 1st turn,	900	micro-mm.
Reissnerian membrane, length of, 2nd turn,	700	,,
Distance between the bases of the pillars of Corti,	66-70	,,
Height of the arches at centre,	12	,,
Cell bodies of the inner hair cells, length,	18	,,
Cell bodies of the inner hair cells, breadth,	6-9	,,
External hair cells: total length with basilar process,	6-7	,,

Number of the foramina nervina,	3,000
,, internal pillars,	4,500
,, internal hair cells,	3,300
,, external hair cells,	18,000

Note.—A micromillimetre = $\frac{1}{1000}$ of a millimetre.

CORNEA.

Cornea proper,	thickness,	1 mm.
Extl. epithelium,	,,	30 micro-mm.
Descemet's membrane,	,,	8-10 ,,

GUSTATORY ORGAN.

Length of gustatory bulb,	80 micro-mm.
Breadth ,, ,,	40 ,,
Width of gustatory pore,	3 ,,

RETINA (*Schultze*).

Rods, length,	60 micro-mm.
thickness,	2 ,,
Cones in fovea centralis: thickness at base,	3 ,,
,, elsewhere,	6 ,,
Distance between cones,	8-10 ,,
Distance between striæ on rods,	·3 ,,

TOUCH.

End bulbs,	= 42 micro-mm.
Pacinian bodies,	= 130 ,,
Touch ,,	= 85 ,,

V.—SPECIFIC GRAVITY of various Constituents of Body—Water = 1000.

Lungs,	342	Serum,	1026
Fat,	924	Milk,	1030
Sweat,	1004	Grey matter of brain,	1034
Saliva,	1006	White ,,	1040
Cerebro-spinal fluid,	1006	Cartilage,	1050
Liquor amnii,	1008	Kidney,	1052
Intestinal juice,	1011	Blood,	1056
Pancreatic ,,	1012	Liver,	1056
Muscle,	1020	Fœtal lungs,	1056
Urine,	1020	Spleen,	1060
Bile,	1020	Body (entire),	1065
Lymph,	1020	Blood corpuscles,	1088
Gastric juice,	1023	Bone,	1900
Chyle,	1024		

APPENDIX D.

ON THE MEASUREMENT OF THE CURVATURES OF THE CORNEA AND LENS, AND THE USE OF THE OPHTHALMOMETER.[1]

THE cornea being a refractive and reflecting structure, acts both as a lens and as a convex mirror. It acts as a lens by refracting to a slight extent rays of light passing through it, and it acts as a convex mirror by reflecting rays of light from its surface. It is the latter property that is taken advantage of in the method of making accurate measurements of its radius of convexity.

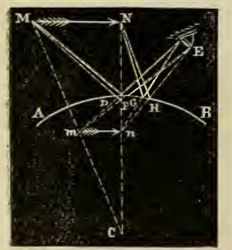


FIG. 201.—Reflection by a convex mirror.

Formation of Images by Convex Mirrors.—The image produced by a convex mirror is an erect image apparently placed behind the mirror. This will be understood by referring to Fig. 201. Here A B is a convex mirror, and C is the centre of the circle of which C F is the radius, and A B is an arc. If the eye of the observer be placed at E, a reflected and erect image of the arrow M N will be seen at *m n*, but reduced in size. Of the numerous rays of light reflected from the surface of the mirror, only a few can enter the eye, and those which do, such as D E, F E, G E, and H E, are so reflected that the angles of incidence and reflection are equal. The ray M D is reflected in the direction D E, the angle of incidence M D N being equal to the angle of reflection

---

[1] Written by the Author for Hughes Bennett's Textbook of Physiology.

N D E. The same is true of the rays M F, N H. By carrying back the rays E D, E F, they will be found to meet at the point *m*, and they will appear to an eye placed at E as if they had come from their focal point *m*. In the same way the rays E G, E H, will apparently issue from *n*,—all the points composing the image *m n* being foci conjugate to the points composing the object M N. The small image *m n* will therefore be the virtual image of M N. By drawing the lines M C, N C, it will also be found that the virtual image *m n* is always within those lines, hence the image is erect and always smaller than the object. It is important also to recollect that the size of the image *m n* is to the size of the object M N as the distance of the image from the centre of the mirror *m* C is to C M, the distance of the object. The image *m n* will recede from the surface of the mirror, as the object M N recedes from it, and when the object M N is indefinitely distant, as it often is in the case of objects placed before the cornea, the image *m n* will be situated about half-way between the mirror and C, that is at a point corresponding to half the radius of convexity. It follows also from this, that the greater the degree of convexity of the surface of the mirror, the smaller will be the virtual image, a fact which may be easily demonstrated by comparing the sizes of the reflected images in convex mirrors of different degrees of convexity.

Formula for Calculating Radius of Curvature of Cornea.—When we apply these principles to the cornea, we find that it acts as a convex mirror, having a virtual image behind it at a point situated at a distance of half the radius of its convexity. The size of the image must be measured, and from its size the radius of curvature may be calculated thus:

Let C D in the above figure be the cornea, and E F H its optical axis. The object A B, placed before it, will be reflected by its surface, so that its

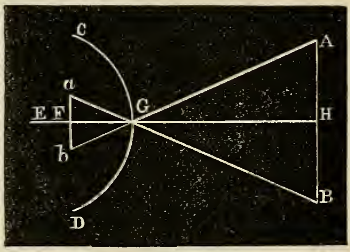


Fig. 202.—Diagram illustrating the estimation of the radius of curvature of a convex reflecting surface.

virtual image will be *a b*, placed at F, that is at a distance of half the radius E G. Draw the lines A *b*, B *b*. The object A B will be to the image *a b* as the distance H G is to G F, that is half the radius. Let R = the radius—

$$\text{A B} : a\,b :: \text{H G} : \text{G F (that is half R)}$$

$$\tfrac{1}{2}\,\text{R} = \frac{\text{H G} \times a\,b}{\text{A B}}$$

$$\text{Or R} = 2\left(\frac{\text{H G} \times a\,b}{\text{A B}}\right)$$

Thus let A B = 1000 mm.; *a b*, 1 mm.; and H G, 3800 mm.; what is the radius of curvature?

$$\tfrac{1}{2}\,\text{R} = \frac{3800 \times 1}{1000} = 3{\cdot}8$$

$$\text{R} = 3{\cdot}8 \times 2 = 7{\cdot}6 \text{ mm.}$$

Optical Principles of the Ophthalmometer.—The instrument by means of which we measure the size of the reflected image on the convex surface of the cornea or lens is termed the Ophthalmometer (οφθαλμος, the eye; μετρον, a measure). This ingenious instrument was invented by Helmholtz. In order to

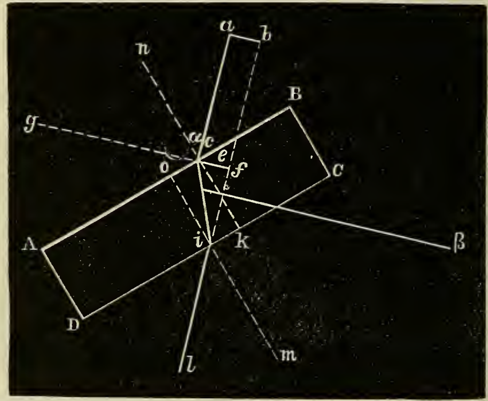


FIG. 203.—Diagram illustrating the optical principles of the Ophthalmometer.

understand its practical application, it is necessary, in the first instance, that we examine the optical principle on which it is constructed. When a ray of light falls perpendicularly on the surface of a glass plate, it passes through it without undergoing any refraction. If, however, the plate be held obliquely to the direction of the ray, as seen in the accompanying figure, we obtain a different result.

Here A B C D in the above figure represent a plate made of flint glass, having the ray *a c* impinging upon its surface. It is refracted in the direction *c i*, and on passing again from the flint glass into the air, it is a second time refracted in the direction *i l*,—*i l* being parallel with *a c*. Draw a line perpendicular to A B, namely *n c*, and continue it to *k*. The angle *a c n* is equal to the angle *m i l*, being produced by parallel lines falling on parallel surfaces. The angle α bears a ratio to the angle β,—the angle of refraction. The index of refraction of flint glass is 1·6. Hence the sine of the angle $a = 1{\cdot}6\ (\sin\ \beta)$. Consequently, if the eye be situated at *l*, the point *a* will not be seen at *a*, but at *b*, in the direction of the line *l f b*. The glass plate, therefore, effects a *displacement* of the point *a* to the right, and to an extent indicated by the length of the line *a b*. As yet we do not know the length of *a b*, but it may be represented by the line *c f*, which is equal to *a b* by parallel lines. The line *c f* we will term *e*. In the triangle *c f i*, *c f* is opposite to the angle *c i f*, and *c i* is the hypothenuse, therefore—

$$\frac{e}{c\,i} = \sin\ c\,i\,f.$$

and therefore

$$e = c\,i\,.\,\sin\ c\,i\,f.$$

But *e* has not yet been measured, neither do we know the length of *c i*, nor the angle *c i f*. We must now find *c i*. This line is, as the figure shows, the hypothenuse of a triangle *c i k* ; and one of the sides of this triangle, *c k*, is equal to the thickness of the glass plate, which we will term P. The line *c k* is adjacent to the angle *c i k*, and hence we get

$$\frac{\mathrm{P}}{c\,i} = \cos\ \beta.$$

by multiplying $c\,i$, we have

$$P = \cos\beta \,.\, c\,i,$$

wherefore

$$c\,i = \frac{P}{\cos\beta}\,.$$

Now we know that P equals the thickness of the glass plate, and that the sines of the angles α and β are in a known ratio. But by substituting the value of $c\,i$ in the previous equation, we have

$$e = \frac{P}{\cos\beta}\ \sin c\,i\,f.$$

We see now that the $c\,i\,f$ equals $h\,i\,f - h\,i\,c$; but $h\,i\,f$ equals the angle of incidence α, in that their sides are parallel; and $h\,i\,c$ equals the angle of refraction β, because they are alternate angles. Therefore $c\,i\,f$ equals $\alpha - \beta$, and $\sin c\,i\,f = \sin\,(\alpha - \beta)$. We have therefore the following formula: (e representing the amount of displacement of the point a towards b, and P the thickness of the plate).

$$e = P\,\frac{(\sin \alpha - \beta)}{\cos\beta}\,.$$

But as there are two such plates in the ophthalmometer, we have the complete formula, in which E will equal the total displacement.

$$E = 2\,P\,\frac{\sin\,(\alpha - \beta)}{\cos\beta}\,.$$

The use of the ophthalmometer, therefore, is to supply us with the angle α, and as we know the thickness of the glass plates, and the index of refraction between air and flint glass (namely 1·65), by applying the above formula, the amount of lateral displacement may be ascertained. Suppose the thickness of the glass plate to be ·325 mm., the index of refraction 1·65, and the angle of incidence 6°, we find, by the use of logarithmic tables, that $\beta = 3^\circ\,37'$, very nearly. Therefore $\alpha - \beta = 6^\circ - 3^\circ\,73'$ $= 2^\circ\,23'$. This gives, on referring to the tables, $e = 0{\cdot}027$ mm. very nearly.

Description of the Ophthalmometer.—This instrument consists of a telescope suitable for short distances. It is illustrated by Fig. 204. The axis of the telescope coincides with the plane of separation of the two glass plates B B, C C. If with this instrument we look at an object of the size X Y, and turn the glass plates so that the two images *x y*, *x y* touch, the size of the image X Y will be half the distance between the points *x* and *y*, a distance which can be ascertained by measuring the angular displacement of the two plates. In the fig. to the left, it will be seen how the ray proceeding from A is deflected in passing through the plates B B, C C, so that an eye placed at the position of the upper A would see the lower A not at *e* but at A, that is a little to one side.

Mode of using the Ophthalmometer.—The first requisite for ophthalmometric observations is a room having the walls blackened, and from which all sunlight can be excluded. The ophthalmometer is placed at a distance of ten feet from the eye under examination, and on a level with it. The object to be reflected on the cornea, until recently, was the distance between three candle flames placed beside the experimenter, two being on his right hand and one on his left. Woinow has, however, now substituted for this an apparatus consisting essentially of three small *rectangular mirrors* fixed by universal joints to a graduated wooden rod about four feet long. The distance between the mirrors may be regulated by sliding them in moveable sockets along the rod. In the centre of the rod there is a circular movement round a graduated scale, so that the rod may be placed vertically, obliquely, or horizontally, according as it may be desirable to obtain images in a vertical, oblique, or horizontal

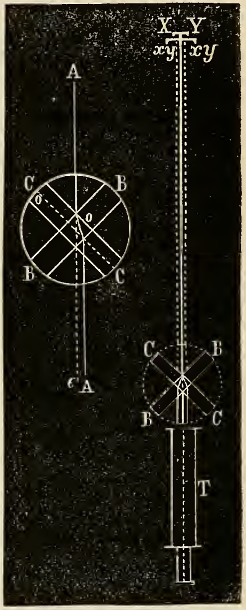


FIG. 204.—Ophthalmometer of Helmholtz. See text.

meridian of the cornea. This mirror-apparatus is screwed to a table immediately in front of the ophthalmometer. A candle flame is now placed on the right or left hand side of the eye to be examined (for the right eye on the right side and for the left eye on the left), as near it as possible, and on the same plane, a dark screen intervening, so as to protect the eye from the glare of light. The experimenter now throws, by means of the mirrors, a reflection of the light from each mirror upon the eye. He then places his own eye to the telescope of the ophthalmometer, and by carefully focusing the instrument, and directing it to the eye under observation, he sees three minute specks of light, thus * * * on the cornea. The vernier of each scale of the ophthalmometer is now at zero. Then, by turning rotating screws, the glass plates in the interior of the box are placed obliquely, and the motion is continued until six small specks of light are seen thus :—

*	*	*	*	*	*
1	*a*	2	*b*	3	*c*

Here the asterisks numbered 1, 2, 3, represent one-half of the amount of displacement in the one direction, and those marked *a*, *b*, and *c*, half the displacement in the other direction. Thus the three original images have been displaced through a distance equal to that between the two extreme images. The number of degrees through which the plates have moved are now read off, giving the angle of incidence, and by means of the calculation above described, the size of the image is ascertained. The following measurements are now made : First, the distance between the upper and lower reflecting mirrors—this gives the size of the object ; and second, by a tape line divided into millimetres, the distance from the anterior surface of the cornea to the centre of the apparatus bearing the mirrors ; but as these reflect rays of light from the candle flame, this measurement must be doubled. We now know the size of the object, the size of the image, and the distance of the object from the cornea ; and from these data, by the formula already given, the radius of curvature is easily calculated. (For an example, see p. 720).

Donder's Method of using the Ophthalmometer.—This is an easier, though a less accurate, mode of measuring reflected images. It consists of preparing a scale, in which each degree, or fraction of a degree corresponds to a certain size in millimetres. The mode of constructing it is as follows: Place a small white ivory scale, divided into tenths of a millimetre, at a distance of ten feet from the ophthalmometer. Turn the plates until the lines on the scale diverge and ultimately pass through any given distance, say $\frac{1}{10}$ of a millimetre, $\frac{1}{8}$, $\frac{1}{6}$, $\frac{1}{4}$, $\frac{1}{3}$, $\frac{1}{2}$, $\frac{3}{4}$, or 1 millimetre. The number of degrees corresponding to each of these displacements is noted, and thus a scale, by numerous observations, may be readily constructed. Observations are to be made on the living eye as described. When the distance between two reflections on the cornea, representing the images has been displaced through its whole extent, the number of degrees are noted, and on referring to the scale of measurement prepared as above, the size of the image is at once known.

Measurements made by means of the Ophthalmometer.—We give here various measurements in millimetres made by means of the ophthalmometer, which are intended to serve as standards of comparison for students or others who may make a special study of, and devote time to, the subject :[*]

OPTICAL CONSTANTS.	Myopic eye. *Knapp.*		Hypermetropic eye. *Woinow.*		Presbyopic eye. *Adamück and Woinow.*	
	Rest	Accommodation.	Rest.	Accommodation.	Rest.	Accommodation.
Radius of cornea, . .	7·2053	7·2053	8·00747	8·00747	7·15568	7·15568
Radius of anterior surface of lens, . . .	9·0641	5·0296	9·3785	5·2904	10·2021	8·5975
Radius of posterior surface of lens, . .	6·4988	5·0855	6·2480	4·9714	6·2156	5·0001
Distance of anterior surface of lens from the cornea, . . .	3·4786	2·8432	3·6175	3·0028	3·23731	2·98985
Thickness of the lens, .	3·6225	4·2579	3·5825	4·1972	3·96269	4·21015
Focal distance of the lens,	43·133	30·939	44·9616	31·185	46·357	38·1513
Index of refraction of the cornea, aqueous humour and vitreous humour, .	1·3465[†]	....	....	....	....	....
Index of refraction of the lens, ...	1·4545[†]	....	....	....	....	....

---

[*] M. Woinow, Ophthalmometrie, Wien, 1871. [†] Helmholtz, Physiologische Optik.

APPENDIX E.

ON SOME OF THE OPTICAL ARRANGEMENTS OF THE EYE.[1]

These have been described generally at p. 565, but there are certain theoretical points not discussed in sufficient detail to be of much practical use, but which ought to be familiar to every student of physiological optics.

1. *The Calculation of the Focal Distance of a Lens.*—The distance of the focal point depends on (*a*) the refractive power of the lens in relation to the medium from which rays enter it ($n : 1$); (*b*) the degree of convexity of the two surfaces of the lens, which is expressed by the length of the radii of the spheres of which they form a part; and (*c*) on the distance of the object from the lens. The formula for the focal distance is—

$$\frac{n-1}{f} + \frac{n-1}{g} = \frac{1}{a} + \frac{1}{\alpha}.$$

Here n = the refractive power of the lens, or the ratio of the sine of the angle of incidence to the sine of the angle of refraction, which, in the case of glass receiving rays from air, is 3 : 2 or $\frac{3}{2}$. For air and glass, therefore, $n - 1 = \frac{3}{2} - 1$. Again, f and g are the radii of the convexities of the lens; a is the distance of the luminous object from the lens, and α is the desired focal distance. Suppose rays to pass from air into a glass lens, the

---

[1] In arranging this part, the author has made use chiefly of Müller's Physiology and Wundt's Physique Médicale.

radii of the convexities of which are 10 and 12 millimetres, and the distance of the lens from the luminous point 100 millimetres, then—

$$\frac{\frac{3}{2}-1}{10}+\frac{\frac{3}{2}-1}{12}=\frac{1}{100}+\frac{1}{x} \text{ or } \frac{3}{2}-1\left(\frac{1}{10}+\frac{1}{12}\right)=\frac{1}{100}+\frac{1}{x}.$$

For parallel rays, as the distance of the luminous point may be considered as infinite, $\frac{1}{a}=0$, and the formula for finding the focal distance will be

$$\frac{n-1}{f}+\frac{n-1}{g}=\frac{1}{\alpha};$$

or if α be used to designate the focal distance for diverging rays, the formula for the focus of parallel rays will be

$$\frac{n-1}{f}+\frac{n-1}{g}=\frac{1}{p}.$$

Again, if we combine the formulæ for finding the focal point of diverging rays with that for the focal point for parallel rays, half of each equation is got rid of, as it is the same, and we have

$$\frac{1}{p}=\frac{1}{a}+\frac{1}{\alpha},$$

p being the focal distance for parallel rays, a the distance of the luminous point, and α the focal distance for diverging rays. If we know, then, the focal distance of the lens for parallel rays, and the distance of the luminous point, the equation will be $\alpha=\frac{a\,p}{a-p}$, or "*the focal distance of the image of any luminous point is found by multiplying the distance of the object from the lens by the focal distance for parallel rays, and dividing the product by the difference between them.*"

2. *Refraction and Formation of an Image.*—These may be understood by studying Fig. 205.

Suppose rays to emanate from the object 1, 5, 3, those proceeding from 5, in the directions 5, 10, 5, 9, and impinging on the curved surface 10, 8, 9, having a different refractive power, are reunited at 6, in the direction of the lines 10, 6, and 9, 6; the principal ray, 5, 8, is not refracted. The amount of deviation of the other rays depends (1) on the ratio of the rapidity of transmission of light in the two media; and (2) on the angle which each of them makes at the point of incidence with a perpendicular, as at 3, 9, 7. Here 7 is the angle of incidence, and the angle 9, 4, which the refracted ray makes with the normal from the point of incidence, is the angle of refraction. The angle of incidence being α, and the angle of refraction β, the ratio they bear to each other, denominated n, is $n = \frac{\sin \alpha}{\sin \beta}$; and if $n' =$ the index of refraction of the first medium, and n'' that of the second, the ratio is $n = \frac{n'}{n''}$.

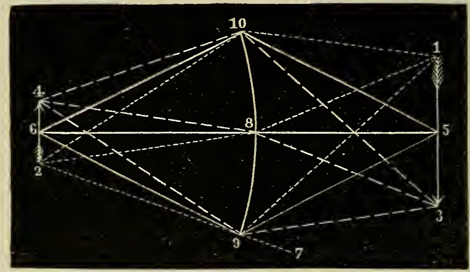


Fig. 205.—The action of a curved transparent surface between two media.

Now, on looking at Fig. 205, it will be seen that the rays from 1, in the direction of 1, 10 and 1, 9, are focused at 4, and those from 3, in the direction 3, 10, 3, 9, at 2. Thus a small and real image, 2, 4, is formed. A *real* image is produced when the luminous rays cross directly; and the image is said to be *virtual* when the rays only cross when prolonged. The points 1 and 2, 3 and 4, may be called conjugated. The line 5, 6 is the optical axis, and the point 5, on this axis, in front of the refractive medium, from whence rays emanate which remain parallel to the axis after refraction, is the anterior focal point; the point behind the refractive medium where rays meet which were parallel before their refraction, is the posterior focal point; and these two points are conjugate.

3. *Action of a Convex Lens.*—The refraction of light by a convex lens depends on the refraction of its two surfaces; but it is to be observed that when a ray, *d e*, as in Fig. 206, passes from a rarer into a denser medium, it *approaches* the normal *a b*, and passes in the direction *e f*; and when it issues from a denser into a rarer medium, it is bent *from* the normal *c b* in the direction *f g*. Consequently, we may replace the action of one lens by that of another having surfaces of a greater degree of convexity, or by one having a greater refractive power. Such lenses form small and reversed images of distant objects.

4. *Certain Optical Measurements and Values as regards the Eye.*

a. *The Cornea and Lens.*—Its curvature is a curve in which all the meridians passing through the centre have nearly an

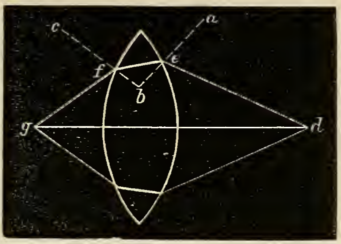


Fig. 206.—A convex lens.

elliptical form, and in which the radius of curvature from the summit of each ellipse is nearly constant. The mean radius is 7·5 mm. The radius of curvature of the anterior surface is from 7 to 9 mm., and that of the posterior from 5·3 to 6·9 mm. The distance of the summit of anterior surface of the lens from that of the cornea is 2·9 to 3·1 mm.; that from the posterior surface of lens to cornea, 7·1 to 7·5 mm.; and the thickness of the lens, 4 to 4·6 mm. Helmholtz, Knapp, and Woinow have made elaborate measurements of the radii of curvature, etc., of the cornea in different meridians, so as to ascertain its exact form. Knapp has shown that the curvature of the vertical meridian does not coincide exactly with that of the horizontal meridian. Thus, in the following table, which gives Knapp's measurement in mm. of the cornea of a lad of fifteen years of age, $r =$ the radius of curvature in the vertical axis, and r^1, $r^2 = 2$ radii at points situated 21° 15′ to the right, to the left, and above and below the summit of the cornea:—

	r.	r_1.	r_2.
Horizontal, . .	8·0668	8·2802	8·8148
Vertical, . .	8·2572	8·6929	8·7856

b. *Refractive Powers of the various Media.*—The following table gives the indices of refraction found by Sir David Brewster, Krause, and Helmholtz; $n =$ the index of refraction of distilled water:—

					LENS.		
	n.	Cornea.	Aqueous.	Vitreous.	External Layer.	Middle Portion.	Nucleus.
Brewster,. .	1·3358	..	1·3366	1·3394	1·3767	1·3786	1·3839
Krause, . .	1·3342	1·3507	1·3420	1·3485	1·4053	1·4294	1·4541
Helmholtz, .	1·3354	..	1·3365	1·3382	1·4189	..	..

Helmholtz found in two cases the *focal distance* of the lens bathed in the aqueous humour to be 45·144 mm. and 47·435 respectively.

5. *The Cardinal Points or Constants of the Eye.*—These are: (*a*) *two focal points.* Every ray which, before refraction, passes through the *first* focal point, becomes, *after* refraction, parallel to the axis; every ray which, before its refraction, is parallel to the axis, passes after refraction through the *second* focal point; and all rays passing through a perpendicular plane cutting the axis at the first focal point are parallel after refraction; (*b*) *two principal points:* every ray passing through the first point before refraction, passes through the second after refraction, and every ray which passes through any point in a plane perpendicular to the axis at the first principal point, passes through a corresponding point in an analogous plane cutting the axis at the second principal point; the second principal plane is therefore the image of the first principal plane; (*c*) *two nodal points;* and (*d*) focal lengths, for a definition of which see p. 566.

6. *The Course of Rays through such an arrangement.*—This may be studied with the aid of Fig. 207. Let 8 and 9 be the

two focal points, 10 and 11 the two principal points, and 13 and 14 the two nodal points; then (1) a ray, 1, 4, meeting the first principal plane, 4, meets the second principal plane at 5; (2) a ray, 1, 13, directed to the first nodal point, after refraction, is 14, 15, passing through the second nodal point parallel to its first direction; and (3) two rays, 3, 4 and 3, 12, passing from 3 through the first focal plane, are parallel after refraction, and become 5, 6 and 3, 12.

With these principles, it is not difficult to determine the direction taken by any ray after refraction, and the point where any luminous object forms its image. Suppose 1, 4 to be the ray which we wish to trace after refraction: draw a perpendicular line from 4, where the ray strikes the first principal plane, and we reach 5, or the second principal plane; after refraction, therefore, the ray will pass through the point 5. Then fix the point 3 from whence the ray, before refraction, cuts the principal focal plane. From 3, also, another ray 3, 13 passes to the first nodal point 13, and after refraction is continued as 14, 7. But, as above stated, all rays passing through the point 3, in the first focal plane, are always parallel after refraction, and the ray 1, 4 is, therefore, after refraction, parallel to 3, 12. The ray 1, 4 must pass through 5, and its direction after refraction will be 5, 6. Again, from the point 2 there is a ray 2, 16, parallel to the axis, and a second ray, 2, 11, passing through the first nodal point. The ray 2, 16, passing from 16, situated in the second principal plane, comes to a focus at 9; the ray 2, 13

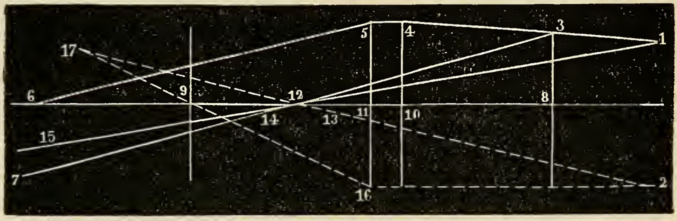


FIG. 207.—Diagram showing the course of rays of light through a refractive medium.

becomes 2, 17 after its refraction; and the two rays, 2, 16, 17 and 2, 13, 17, meeting at 17, will form there an image of the point 2.

7. *The Schematic Eye.*—Listing has, from a consideration of the radii of curvature of the refractive surfaces, and of the index of refraction of these media, determined these 6 cardinal points with reference to the human eye, and has thus theoretically constructed an ideal or schematic eye. The measurements in millimetres from the summit of the cornea of such an eye are—

First principal point, . . .	2·1746	Difference 0·3978
Second principal point, . . .	2·5724	
First nodal point, ...	7·2420	Difference 0·3978
Second nodal point, . . .	7·6398	
Anterior focus, ...	12·8326	
Posterior focus, ...	22·6470	
Anterior focal length, . . .	15·0072	
Posterior focal length, . . .	20·0746	

Considering the very short distance between the two principal points, only 3978 mm., a *simpler* or *reduced* theoretical eye may be formed having the following measurements: Principal points, 2·3448 mm., behind summit of cornea; nodal points, 7·4969 mm.;

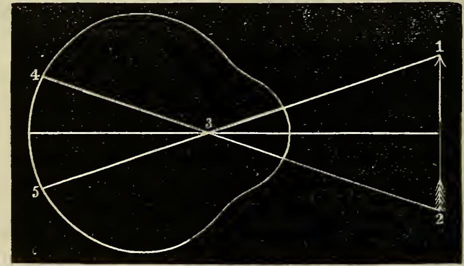


Fig. 208.—Diagram showing line of ray of direction, &c.

anterior focal length, 15 mm.; posterior focal length, 20 mm.; refracting surface, having a radius of curvature of 5 mm., is 3 mm. behind cornea, and refractive index is $\frac{4}{3}$.

8. *Terms used in reference to Direction of Rays.*—In Fig 208, a reversed image of 1 2 will be formed on the retina at 4 5.

The lines passing through the nodal point 3 are the lines of direction ; it will be observed that the lines of direction *cross* at the nodal point. The ray which falls on the yellow spot, that is in the field of distinct vision, is the visual axis. It is situated about 2 degrees to the inner side, and a little above the optical axis of the eye. By following the path of the lines of direction, we can understand how an image is formed on the retina, but they do not accord with those along which we project our sensations into the outer world. These may be termed the lines of sight, and the angle they form is the *visual angle.*

9. *Measurement of Acuteness of Vision.*—This is done by employing letters of various sizes which are read with a visual angle determined by the distance *d.* Such types as those of Jaeger and Snellen are of such a size as to be seen distinctly by a normal eye at a certain distance, D, usually expressed as 3, 4, 6, or 15, &c., Paris feet; all in an angle of 55 minutes. Acuteness of vision, A, is expressed thus, $A = \frac{d}{D}$. $d = D$ would of course express normal vision.

10. *Degree of Astigmatism.*—This is measured by the difference of the refraction of the two chief media. Thus, if f^1 = the greater focal length and f^2 = the smaller, then the amount of astigmatism will be $AS = \frac{1}{f^1} - \frac{1}{f^2}$. The optical correction for astigmatism is made by cylindrical glasses which act only on *one* of the meridians. If $\frac{1}{f}$ = the refractive power of the lens, this added to that of the meridian of the minimum of curvature, will make the focal length equal to that of the meridian of the maximum of curvature. When the amount of astigmatism does not pass $\frac{1}{40}$, it is regarded as normal and no glasses are employed.

APPENDIX F.

RELATION OF METRIC SYSTEM TO ENGLISH MEASURES.

Capacity.

1 Litre, . . . = $1\frac{3}{5}$ pints.
4·54 Litres, . . = 1 gallon.

Linear Measure.

1 Metre, . . . = 39·3 inches.
25·4 Millimetres, . = 1 inch.
3·05 Decimetres, . = 1 foot.
1 Centimetre, . . = $\frac{2}{5}$ of an inch.
1 Decimetre, . . = 3·93 inches.

Weight.

1 Gramme, . . = 15·43 grains.
1 Kilogramme, . . = 32·15 Troy ounces, or 35·27 Avoirdupois ounces.
0·065 Gramme, . . = 1 grain.
31· Grammes, . . = 1 ounce.
0·45 Kilogramme, . = 1 pound Avoirdupois.

Note.—Many of the measurements in this volume have been given according to the metric system. In the author's opinion, it would be a great gain if this system were adopted in all scientific treatises in this country. At present, it is difficult for the student to form accurate ideas of dimensions, weights, and of capacity in the terms of the metric system, as his teachers in the preliminary subjects frequently do not employ it. The author has therefore given the above rough table, and he would refer the student for details to Hofmann's Lectures on Chemistry, 1865, where he will find a complete account of the principles of the metric system, which, from its simplicity, readiness of manipulation, and acceptance by scientific men in all countries, ought to be generally adopted.

INDEX.

ROBERT MACLEHOSE, PRINTER, GLASGOW.

ERRATA.

Page	6,	line	9,	for “or” read “nor.”
,,	9,	,,	21,	for “animal” read “mineral.”
,,	12,	,,	13,	for “is” read “are.”
,,	18,	,,	16,	delete “a.”
,,	26,	,,	22,	for “butter” read “sweat.”
,,	84,	,,	14,	for “three” read “three fourths.”
,,	85,	,,	26,	for “K” read “Na.”
,,	166,	,,	18,	for “anelectrotonous” read “anelectrotonus.”
,,	312,	,,	7,	for “left” read “right.”
,,	324,	,,	17,	for “35” read “7.”
,,	324,	,,	18,	for “100” read “50.”
,,	341,	,,	38,	for “movement” read “mouvement.”
,,	408,	,,	30,	for “Parke’s” read “Parkes’.”
,,	416,	,,	14,	for “adipocire” read “adipocere.”
,,	483,	,,	2,	for “upward” read “downward.”
,,	483,	,,	4,	for “downward” read “upward.”
,,	502,	,,	12,	for “annelidæ” read “annelida.”
,,	502,	,,	29,	for “crustaceæ” read “crustacea.”
,,	566,	,,	11,	after “axis” insert “after refraction.”
,,	566,	,,	12,	for “these” read “the.”
,,	566,	,,	13,	after “point” insert “after refraction.” See also p. 730.
,,	566,	,,	35,	for “opthalmometer” read “ophthalmometer.”
,,	642 and 643,			vibrations given are double vibrations.

WORKS PUBLISHED BY MR. MACLEHOSE,

Publisher to the University of Glasgow.

LECTURES on the GRAPHIC METHOD of PHYSIOLOGICAL RESEARCH, Illustrated by numerous Engravings, by JOHN GRAY M'KENDRICK, M.D., F.R.S.E., Professor of Physiology in the University of Glasgow. Small 8vo. [*Shortly.*

CREED AND CONDUCT: Sermons preached in Rosneath Church by the REV. ROBERT HERBERT STORY, D.D., Minister of the Parish. Crown 8vo., Cloth Price 7s. 6d.

HILDA, AMONG THE BROKEN GODS: A Poem by the Author of "Olrig Grange." Small 8vo. [*In the press.*

A SYSTEM OF MIDWIFERY, Including the DISEASES OF PREGNANCY AND THE PUERPERAL STATE. By WILLIAM LEISHMAN, M.D., Regius Professor of Midwifery in the University of Glasgow. In One Thick Volume, Demy 8vo, nearly 900 pp., with 183 Wood Engravings. A new and cheaper Edition, enlarged and thoroughly Revised, Price 21s.

"We can strongly recommend the work as unquestionably the best modern book on midwifery in our language."—*British and Foreign Medico-Chirurgical Review.*

"We have no hesitation in saying that we recommend this work to the student desirous of mastering the difficult subject of obstetrics, in preference to any other English work in existence.—*Medical Press and Circular.*

"We have little hesitation in saying that it is, in our judgment, the best English work on the subject."—*Lancet.*

A CRITICAL ACCOUNT OF THE PHILOSOPHY OF KANT, With an Historical Introduction, by EDWARD CAIRD, M.A., Professor of Moral Philosophy in the University of Glasgow, and late Fellow and Tutor of Merton College, Oxford. One Vol., Demy 8vo, cloth, 650 pp., Price 18s.

"At last we have in English a book which will tell any one accustomed to philosophical reading, and who will read it with attention, what it was that Kant had to say, how he came to say it as he did, and how what he said has had such a different significance for different inquirers. Mr. Caird's statement of the Kantian doctrine is singularly felicitous. The simplification is at once full, accurate, and unbiassed."—T. H. GREEN, in the *Academy.*

"No account of Kant's Philosophy has ever appeared in England so full, so intelligible, and so interesting to read as this work by Professor Caird. It is *the* English book on Kant."—*Contemporary Review.*

"It is the best book on Kant's 'Philosophy' that I am acquainted with, either in our own language or in German, and cannot fail to be the standard work upon the subject for a long time to come. . . . . Mr. Caird has made solid additions to English philosophy and psychology."—*Mind.*

THE TREATMENT OF SPINA BIFIDA BY A NEW METHOD. By JAMES MORTON, M.D., Professor of Materia Medica, Anderson's University, and Surgeon and Clinical Lecturer of Surgery in the Glasgow Royal Infirmary. In One Volume, Crown 8vo, with Six Illustrations, Cloth, Price 5s.

THE HISTORY AND POETRY OF THE SCOTTISH BORDER; their Main Features and Relations. By John Veitch, LL.D., Professor of Logic and Rhetoric in the University of Glasgow. Cr. 8vo, Price 10s. 6d.

"This is a genuine book. We can heartily recommend it to three classes of readers; to all who have felt the power of 'Scott's Border Minstrelsy' (and who with a heart has not?); to all who care to visit and really to know that delightsome land—for no other book except the 'Border Minstrelsy' itself will so open their eyes to see it; to all dwellers in the Borderland who wish to know as they ought to know what constitutes the grace and glory of their Borderland."—Prof. Shairp in the *Contemporary Review.*

LUCRETIUS AND THE ATOMIC THEORY. By John Veitch, LL.D., Professor of Logic and Rhetoric in the University of Glasgow. One Vol., Crown 8vo, Cloth, Price 3s. 6d.

"We have read this little volume with no ordinary delight. Not only does Professor Veitch bring out prominently the drift of the philosophy of Lucretius, but he never fails to carry with him that rare and refined poetic sympathy, without which commentary on such a theme becomes hackneyed and lifeless. But it is not in separate arguments or points, however able, that the great merit of the book lies. It is in the fine spirit, the concern for truth and fairness, the poetic sympathy and the grace of patient culture which it bears throughout. On this account we warmly recommend it."—*Nonconformist.*

HILLSIDE RHYMES. By John Veitch, LL.D., Professor of Logic and Rhetoric in the University of Glasgow. Extra Fcap. 8vo, Cloth, Price 5s.

"Next to an autumn day among the hills themselves, commend us to poems like these, in which so much of the finer breath and spirit of those pathetic hills is distilled into melody."—*Scotsman.*

THE TWEED, AND OTHER POEMS. By John Veitch, LL.D., Professor of Logic and Rhetoric in the University of Glasgow. One Vol., Small 8vo, Cloth, Price 6s. 6d.

"The Tweed contains passages which are in themselves complete poems, suffused with quiet thought and coloured with the subdued tints of fancy, deepened by loving and constant association with the great presences of nature which poets have always been prone to magnify."—*British Quarterly Review.*

SONGS AND FABLES. By William J. Macquorn Rankine, late Professor of Civil Engineering in the University of Glasgow. With Portrait, and with Ten Illustrations by J.B. (Mrs. Hugh Blackburn). Second Edition, Extra Fcap. 8vo, Cloth, Price 6s.

"These songs are exceedingly bright, strong, and clever; quite the best we have seen for long. They are, in our judgment, far superior to those of Mr. Outram and Lord Neaves. . . . An admirable photograph is prefixed to the volume."—*Aberdeen Journal.*

THE PIPITS. A Companion Volume to "Caw, Caw," with Sixteen page Illustrations by J. B. (Mrs. Hugh Blackburn.) 4to, Price 3s.

"This is a charming Fable in verse, illustrated by the well-known J. B., whose power in delineating animals, especially birds, is scarcely inferior to Landseer or Rosa Bonheur."—*Courant.*

BIRDS DRAWN FROM NATURE. By J. B. (Mrs. Hugh Blackburn.) Forty-five Plates, Descriptive Letterpress, Imperial 4to, Price £1, 11s. 6d.

HISTORY OF THE CLYDE TO THE PRESENT TIME. With Maps and Diagrams. New Edition Enlarged. By James Deas, Esq., M. Inst. C.E., Engineer of the Clyde Navigation. 8vo, Cloth, Price 10s. 6d.

"It has been attempted in the following pages to tell the story of the improvements which have made the River and Harbour what they are, and to show that they have raised the City of Glasgow from an obscure salmon fishing village to the position of one of the great commercial centres of the world."—*From Author's Preface.*

"Mr. Deas tells his story in a very clear and concise way."—*Saturday Review.*

TABLES OF ANCIENT LITERATURE AND HISTORY, from B.C. 1500 to A.D. 200. By Professor Nichol. Uniform with above, 4s. 6d.

"They constitute a most successful attempt to give interest to the chronology of literature, by setting before the eye the relation between the literature and the practical life of mankind."—*Observer.*

TABLES OF EUROPEAN LITERATURE AND HISTORY, from A.D. 200 to 1876. By John Nichol, LL.D., Professor of English Language and Literature, University of Glasgow. Second Thousand, 4to, Cloth, Price 6s. 6d.

"Clear, and form an admirable companion."—*Times.*

"Very clear."—*Westminster Review.*

THE POETICAL WORKS OF DAVID GRAY. Edited by Henry Glassford Bell, late Sheriff of Lanarkshire. New and Enlarged Edition, Extra Fcp. 8vo, Price 6s., Cloth.

"This volume possesses a peculiarity, independent of the gems which it embodies, in that the editing of it was the last literary labour of the late lamented Sheriff of Lanarkshire. The reverential vigour which pervades the equable verse of David Gray is, however, unique; there is a more forcible beauty in his pieces than in those of the Westmoreland poet, and the awe he manifests 'for things unseen and eternal' is quite as conspicuous as the deep and steady devotion of the poet of the 'Seasons.' The volume is got up with sufficient taste not to befool the precious things within."—*Edinburgh Courant.*

OLRIG GRANGE; a Poem in Six Books. Edited by Hermann Kunst, Philol. Professor. Second Edition, in Extra Fcap. 8vo, Cloth, Price 6s. 6d.

"The story itself is very simple, but it is told in powerful and suggestive verse. The composition is instinct with quick and passionate feeling, to a degree that attests the truly poetic nature of the man who produced it. It exhibits much more of genuine thought, of various knowledge, of regulated and exquisite sensibility. The author exhibits a fine and firm discrimination of character, a glowing and abundant fancy, a subtle eye to read the symbolism of nature, and great wealth and mastery of language, and he has employed it for worthy purposes."—*Spectator.*

BORLAND HALL; a Poem in Six Books. By the Author of "Olrig Grange." Second Edition, Extra Fcap. 8vo, Cloth, Price 7s.

"Lyall's mother, stern and unrepentant, even in death, is a terrible portrait. . . . Such a poem as this will surely have a distinct influence over social thought and custom, for the lessons inculcated have the added weight and enforcement of a style singularly brilliant and passionately fervent, a verse melodious and varied in measure, a command of language unusually extensive and apt, and an exquisite sensibility to all natural loveliness."—*English Independent.*

A MANUAL OF NAVIGATION. By Robert A. Napier, Lieut. R.N.R. Royal 8vo, Cloth, Price 5s.

WORKS PUBLISHED BY MR. MACLEHOSE.

THE LIFE OF A SCOTTISH PROBATIONER; being Memoi of Thomas Davidson. With his Poems and Letters. By the Rev. Jam Brown, Paisley. Second Edition, Enlarged. With Portrait. Crown 8v Price 7s. 6d.

"This Life of an unknown Scotch Probationer is equal in interest to anything of the kind w have had since Carlyle's 'Life of Sterling' was written. Thomas Davidson, as a poet, as humorist, as a simple, loving, honest, reticent, valiant soul, demands adequate recognition Poetry is genuine and humour is genuine, and the character (that which underlies both) a genuine as the poetry and the humour. The delicate light of a grave and quaint fancifulnes pervades his letters. It would be a sin to break them into fragments."—*Blackwood's Magazine*

"'His poems are as perfect as flowers to birds, and the letters might have been written by Scotch U.P. Charles Lamb.' Such is the judgment pronounced upon the 'Scottish Probatione by one of whom all Scotchmen are proud—Dr. John Brown, author of 'Rab and his Friends,' whose approbation is worth a large measure of common renown."—*Macmillan's Magazine.*

"A charming biography."—*Spectator.*

"Very fresh and interesting."—*Saturday Review.*

"An unspeakable pleasure to a reviewer to come upon a prize such as this."—*Nonconformist*

SERMONS Preached in Trinity Church, Glasgow. By William Pulsfor D.D. Crown 8vo, Cloth, Red Edges, Cheap Edition, 4s. 6d.

"The sermons have much of the brilliancy of thought and style by which Robertson fasci ated his Brighton hearers."—*Daily Review.*

"The preacher, we are made to feel, speaks to us out of the fulness of his own spiritual a intellectual life. He has been under no temptation to borrow, just because he had a message his own to deliver, . . . He is a preacher, because he has been first a thinker."—*Spectato*

OUR LORD'S THREE RAISINGS FROM THE DEAD. By th Rev. Hugh Macmillan, LL.D., F.R.S.E., Author of "Bible Teachings i Nature." Crown 8vo, Price 6s., Cloth.

"He has written a book on one of the most trying themes, which is at once edifying instructive, full of devotional fervour as of fine thought.—*Nonconformist.*

"A spirit of earnest piety pervades the book; its language is simple and unaffected, and abounds in apt and felicitous illustrations.—*Scotsman.*

PRACTICAL EDUCATIONISTS AND THEIR SYSTEM OF TEACHING. By James Leitch, Principal of the Church of Sc land Normal School, Glasgow. Crown 8vo, Price 6s., Cloth.

"Mr. Leitch, in this capital book, presents us, in a compact and well-digested form, with that is of most value in the really practical methods of the greatest men who have formulat and left on record their views on this subject.—*School Board Chronicle.*

"He writes a lively and vigorous style, is not without a sense of humour, praises a criticises with candour and freedom."—*Spectator.*

SIR ISAAC NEWTON'S PRINCIPIA, Reprinted for Sir Will Thomson, LL.D., Late Fellow of St. Peter's College, Cambridge; and Hu Blackburn, M.A., Late Fellow of Trinity College, Cambridge; Professors Natural Philosophy and Mathematics in the University of Glasgow. Crown 4 Cloth. Price £1, 11s. 6d.

"The 'Principia' ought to show in every library of pretension a handsome presence, som what in keeping with the place of honour which it holds in the literary history of science; a thanks are due to the two Glasgow professors, both *alumni*, we are glad to know, of an En University, to whose enterprise we owe this very handsome volume."—*Spectator*

GLASGOW: JAMES MACLEHOSE, Publisher to the Universit
LONDON: MACMILLAN AND CO.

H

h
G
ce

T

by

T

T

ed
re
is
he
de
th

O

sit
na
kn
in
na
po

B

a p
so
sic
ex

A